Effects of habitat degradation on species interactions and reproductive success in an Ecuadorian bird community

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Abstract of the Dissertation

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Interactions between species in groups are often ignored in studies of the effects of anthropogenic change on species' persistence. However, given their global ubiquity, mixed species groups have the potential to be models for community ecology. The purpose of my dissertation was to advance the understanding of the drivers of mixed species flocking behavior in birds, as well as how human disturbance affects these interactions and species' nest survival in a unique and highly threatened landscape in the Tumbesian region of Ecuador. I predicted that interspecific interactions would be disrupted and species would have lower nest survival in vegetation disturbed by small-scale livestock grazing and clearing of trees. Further, I predicted that perceived predation risk would be more important than feeding benefits in explaining flocking behavior. To obtain my results I employed line transect counts, mixed flock observations, foraging observations, vegetation plots, livestock abundance surveys, predatory raptor abundance surveys, arthropod traps, nest searching and monitoring. Based on observations of 431 mixed species flocks, I found habitat disturbance had little impact on these interspecific associations in arid scrub, but that there were large negative impacts in tropical dry forest vegetation. Further, based on observations of 805 nests, the nest survival of most species was more greatly negatively impacted by habitat disturbance in tropical dry forest than in arid scrub vegetation. I also determined that in this region birds are forming mixed flocks primarily to avoid predation rather than to accrue feeding efficiency benefits. However, participants were also able to forage at higher rates when in flocks than when alone or with conspecifics, suggesting that birds gain feeding benefits as a side effect of choosing to be with mixed flocks to avoid predation. My findings highlight the importance of examining multiple factors when attempting to predict species' long term persistence or creating conservation management plans. For example, determining how species richness, abundances, interactions, behavior and reproductive success varied across a landscape consisting of various levels of human disturbance allowed me to gain a more complete picture of species specific and community wide impacts of disturbance in this region.

To everyone who supported me along the way

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Chapter 1 – Introduction

Human induced changes in landscapes are the major cause of species' extinctions and endangerment (King and With 2002, Damschen et al. 2006). Landscapes consisting of varying proportions and configurations of intact and human altered vegetation are omnipresent and, consequently, species must use these novel landscapes (e.g., Graham and Blake 2001, McGarigal and Cushman 2002). Species' use of novel landscapes is likely to increase as the climate continues to change and species tracking their climate envelopes are forced into rural or suburban landscapes (e.g., Hellmann et al. 2008, Hoegh-Guldberg et al. 2008). Therefore, one of the most pressing challenges facing ecologists is to provide managers with meaningful information on how to lessen the threat of continued biodiversity loss; this was the challenge that motivated my dissertation. One way to meet this challenge is to use both theoretical and applied tools from ecology to determine how species are using novel landscapes, in order to more successfully predict their long term persistence. Most studies attempting to predict species' responses to altered landscapes rely on simple indicators such as the abundance or geographic distribution of a species. However, ultimately whether or not a species persists in a landscape depends on its survival and reproductive success throughout the landscape, which in turn depend on many different aspects of the species' biology (Fig. 1). For example, how individuals perceive and use the landscape, which resources they obtain, and their movement and dispersal abilities have all been shown to influence species' survival and reproductive success (Knowlton and Graham 2010). Further, both intra and interspecific interactions are often ignored but can influence habitat choice and access to resources, and ultimately survival and reproductive success. Thus, a more integrative approach considering multiple aspects of species' biology will likely prove more successful at providing a complete picture of how species are likely to respond to human alteration of landscapes. With this in mind, for my dissertation research I linked some of these different aspects of species' biology (Fig. 1), with the goal of gaining a deeper understanding about how human caused habitat degradation will affect species' persistence.

As a starting point, I examined how human alteration of landscapes affects species' behavior, including movement and dispersal abilities, by reviewing and placing into a theoretical framework results from an emerging body of research in behavioral landscape ecology (Knowlton and Graham 2010). I highlighted the potential of each experimental method to quantify different processes, such as habitat selection or resistance, which might be useful to modelers attempting to parameterize predictive models. Next, I determined how human disturbance affects interactions between species and species' reproductive success in a landscape in the unique and highly threatened Tumbesian region of Ecuador. I also published new information on the breeding biology of 14 birds in the region, including completely new egg or nest descriptions for seven species, highlighting how little is known about the birds in my study region (Knowlton 2010). Lastly, I examined the drivers of interspecific interactions in this region, specifically mixed species flocking behavior. In the course of this work I employed many different methods, including line transect counts for bird species richness and abundance, mixed species flock observations, foraging observations, vegetation plots, livestock abundance surveys, predatory raptor abundance surveys, arthropod traps, nest searching and monitoring. In this way I was able to gain a more complete understanding, both theoretically and empirically, of how human alteration of land impacts species' behavior and persistence.

The effects of different types of human land use on species' persistence have been well studied in temperate regions, but these results cannot necessarily be generalized to tropical regions, which have more complex natural landscapes and often suffer from different types of human use. For example, extensive areas of the tropics are undergoing small scale clearing of trees and livestock grazing by rural communities, yet few studies have examined the impacts of these common activities (but see Aerts et al. 2008, Lees and Peres 2008, Matthysen et al. 2008). Reduced nest survival is one of the most common causes of long term population declines of forest birds living in human altered vegetation, often due to an increase in nest predation (Chalfoun et al. 2002, Githiru et al. 2005). Livestock grazing has been shown to reduce vegetation cover and to be associated with increased rates of nest predation in temperate regions (Ammon and Stacey 1997, Walsberg 2005, Heltzel and Earnst 2006). However, little is known about the effects of grazing on the reproductive success of tropical forest birds.

The Tumbesian region of south-western Ecuador and north-western Peru encompasses the great majority of remaining coastal tropical dry forest in South America, and is overlooked in terms of effects of livestock grazing on native fauna. The region has already lost over 95% of its original forest and is now one of the most threatened in the world due to heavy human use, partly in the form of extensive livestock grazing by rural communities (Best and Kessler 1995). The Tumbesian region is among the five most species rich regions of the world in terms of avian endemics (61 species), is home to 32 threatened or near threatened birds, and is considered a critical priority for conservation action (Wege and Long 1995, BirdLife International 2003).

In the Tumbesian region and throughout the tropics, the most common interaction between bird species is mixed species flocking. In these regions flocking often occurs year round and includes a large proportion of the bird community—suggesting that this behavior has a great effect on the fitness of individuals of these species (Hutto 1987, Chen and Hsieh 2002, Maldonado-Coelho and Marini 2004, Pomara et al. 2007). Despite this, relatively little is known about how the costs and benefits of mixed species flocking differ for participating individuals with different roles and across habitat types with differing predator and prey abundances. Species are commonly thought to have evolved to participate in mixed flocks to gain fitness via either: 1) enhanced protection from predators due to earlier warning calls or lower probability of being singled out by a predator; or 2) greater foraging efficiency due to the flushing of insects as the flock moves through an area, kleptoparasatism, or learning new methods of food capture by watching other flock participants; or some combination of both factors (Morse 1977, Munn and Terborgh 1979, Munn 1984, Powell 1985, Terborgh et al. 1990, Jullien and Thiollay 1998). The potential of mixed species groups to be models for community ecology has recently been recognized, and given their global ubiquity these groups offer opportunities for examining universal patterns among communities with different evolutionary histories (Goodale et al. 2010). Therefore, examining interspecific associations across diverse communities is of the utmost importance to both answering basic theoretical questions in community ecology and for conserving species' diversity in the face of anthropogenic landscape change.

For two years I examined the species richness and abundance of mixed species flocks and the bird community as a whole, birds' breeding biology and nest survival in a vegetation and disturbance gradient in Machalilla National Park, the largest park in the Tumbesian region. I also examined feeding efficiencies of birds in and out of flocks and predator and arthropod prey abundances across this landscape.

The specific questions I addressed were:

1) How can experiments in behavioral landscape ecology be used to inform predictive models for conservation? (Chapter 2)
2) How does habitat degradation affect characteristics of mixed species flocks of birds and behavior of individual species in the Tumbesian region of Ecuador? (Chapter 3)
3) How does habitat degradation affect the nest survival of birds in the Tumbesian region of Ecuador? (Chapter 4)
4) What are the specific details of the breeding biology and behavior of birds in the Tumbesian region of Ecuador? (Chapter 5)
5) How do the benefits and costs of participating in a mixed species flock differ depending on a species' role in the flock and across a vegetation type and disturbance gradient in the Tumbesian region of Ecuador? (Chapter 6)

Answering these questions allowed me to explore how species' behavior and persistence is affected by human altered landscapes, test theoretical predictions regarding the drivers of unique species interactions, and gather new information about a little known bird community in a highly threatened region. I found that mixed species flocks of birds in the Tumbesian region display some unique characteristics from flocks in the temperate zone and other tropical regions; that species' responses to habitat degradation are often dependent on vegetation type, even within the same landscape; and that members of mixed species flocks in the Tumbesian region benefit both from increased feeding efficiency and lowered risk of predation, but that different species benefit in different ways. Ultimately, this information can offer valuable insight for managing species in the face of human induced landscape change.

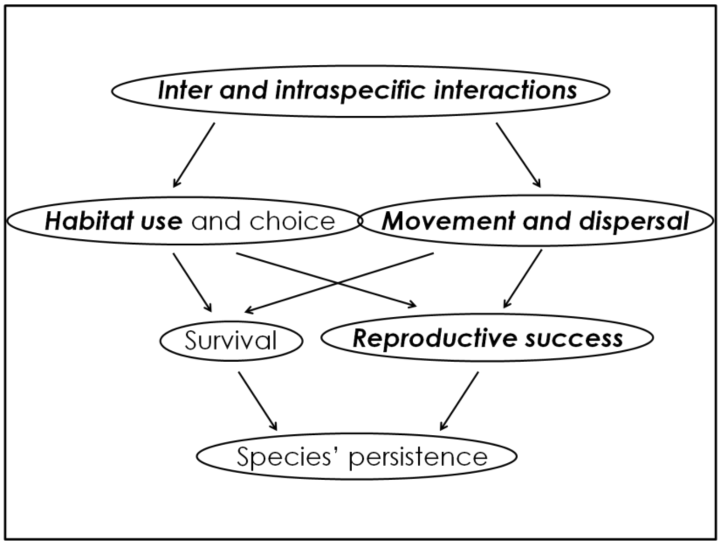

Figure 1. Examples of aspects of species' biology that have been shown to influence survival and reproductive success, and thus species' long term persistence. Inter and intraspecific interactions can be crucial to how an organism moves though and uses a landscape, which in turn affect the organism's survival and reproductive success throughout the landscape. Ultimately, whether or not a species persists in a landscape depends on its survival and reproductive success throughout the landscape. The aspects of species' biology that I examined in my dissertation are in highlighted in bold italics.

Chapter 2 - Using behavioral landscape ecology to predict species' responses to land-use and climate change

Introduction

Human-induced changes in species' habitats are widely recognized as the major cause of species' endangerment (King and With 2002, Damschen et al. 2006). Landscapes consisting of varying proportions and configurations of intact and human-altered vegetation are omnipresent and, consequently, species must use these novel landscapes (Graham 2001, McGarigal and Cushman 2002). Species' use of novel landscape is likely to increase as the climate continues to change and species tracking their climate envelopes are forced into rural or suburban landscapes (Hellmann et al. 2008, Hoegh-Guldberg et al. 2008). To successfully predict if a species will persist in a landscape influenced by land-use and/or climate change requires knowledge of how individuals move or disperse through the landscape, choose habitat in which to settle, and produce offspring which survive to repeat the process (Fig. 1). Ecologists attempting to predict responses of species to landscape and climate changes often lack reliable estimates of these key model parameters (Dunning et al. 1995, Macdonald and Rushton 2003, Zollner and Lima 2005, Vuilleumier and Metzger 2006, Minor et al. 2008). The field of behavioral landscape ecology uses a strong theoretical base to explore, often experimentally, how the behavior of a particular species is affected by heterogeneous and rapidly-changing landscapes and can offer valuable insight for managing species in the face of human-induced environmental changes (Lima and Zollner 1996, Belisle 2005, see Table 1 for landscape ecology term definitions used in this paper).

Empirical and theoretical studies in behavioral ecology have long shown that there are trade-offs associated with individuals' decisions regarding dispersal or movement, habitat selection, and reproduction (e.g., Krebs and Davies 1993). For example, the risk of mortality due to predation or starvation often increases during dispersal or movement away from a familiar area (Vanvuren and Armitage 1994, Schtickzelle et al. 2006, Smith and Batzli 2006, Baguette and Van Dyck 2007). However, selecting habitat that is relatively far away from the natal area can incur benefits, such as decreased risk of inbreeding, greater food or nest site availability, lower predator concentration, or less intra-specific competition. Further, trade-offs often exist between food abundance, predator abundance, nesting site selection, proximity to mates, and so on. Trade-offs associated with reproduction include the amount of parental investment given, number of offspring, number of breeding attempts, time of breeding and mate selection (Reznick 1985, Martin 1995). The costs and benefits of these key behavioral decisions form the basis of many types of models; including metapopulation and individual-based models, and, most recently, graph theoretic models. Metapopulation models aim to predict long-term population persistence based on the behavior of populations within the landscape; movement, dispersal and habitat selection functions determine extinction and recolonization rates (Krebs and Davies 1993, Ruckelshaus et al. 1997). Behavior-based individual-based models are used to determine how the decisions of individual organisms in the landscape influence population demography. Finally, graph theoretic models quantify the connectivity of a landscape for a particular organism and can be used to address a wide variety of ecological, evolutionary and conservation-related questions (McRae et al. 2008, Urban et al. 2009). Therefore, knowledge of which factors influence organisms' decisions associated with the dispersal pattern, habitat selection and reproductive success of individuals is key to realistic outcomes of these and other models used for conservation planning (Ruckelshaus et al. 1997, Alderman et al. 2005, Zollner and Lima 2005, Goss-Custard et al. 2006, Russell et al. 2007). It is clear that the behavioral decisions made by individual organisms will determine their short-term persistence. Further, because these decisions are often based on principles, such as optimization, they may not change in new environments and can be useful for predicting animals' long-term responses to landscape change (Gill and Sutherland 2000). For example, species tracking their climate envelopes may be forced to pass through novel or degraded landscapes (Hellmann et al. 2008, Hoegh-Guldberg et al. 2008).

The last decade has seen a surge of novel methods to examine how species respond to varying landscapes. Specifically, the use of experimentation in landscape ecology is now recognized as important for evaluating of the effects of landscape change on organisms (Desrochers et al. 1999, Belisle 2005). These experiments cover a wide range of taxa—from birds and mammals to reptiles, amphibians and insects. While observational studies are still extremely important, experimentation permits the manipulation of the variable of interest in order to test specific predictions. I discovered six main categories of experimental manipulations in the literature: translocation, playback, landscape alteration, and manipulation of food resources, perceived predation risk, and reproductive success (described below). These experiments result in changes in an animals' location in a landscape, the behavioral cues present in that landscape, or the landscape structure itself. All six types yield information on how behavioral decisions influence movement or dispersal ability, habitat selection and/or reproductive success, and can be used to determine the consequences associated with these decisions (Fig. 1). What is often lacking in the publication of the results of these experiments is a discussion of how the costs and benefits of the observed behaviors can be quantified; allowing modelers to parameratize models in ways that represent biologically meaningful processes. Even if the experiment does not explicitly show the costs or benefits of the behavior, behavioral ecology theory and models can provide the most likely scenarios. Thus, I believe that these experiments, when viewed in light of the costs or benefits of the behaviors, offer many possibilities for modelers to parameratize predictive models and enhance conservation of species in a changing world.

To be accurate, models must represent realistic properties of animals in their environments (Jepsen et al. 2005). Since very little is known about the behavioral factors used to parameterize models, "educated guesses" are made regarding certain parameter values or they are simply left out (Lima and Zollner 1996, Mooij and DeAngelis 2003, Zollner and Lima 2005). This is of particular concern in spatial models—since these models often show important sensitivities for unknown aspects of animal behaviors (Dunning et al. 1995). For example, tests of error propagation in spatially explicit models show that errors in dispersal parameters (which stem from behavioral information) have great consequences for model predictions (Wennergren et al. 1995, Ruckelshaus et al. 1997, Ruckelshaus et al. 1999). Experimentation in behavioral landscape ecology can help quantify the processes associated with animal behaviors and their associated costs; which, when interpreted by experienced modelers, can enhance the predictive power of models (Table 2). For instance, experiments can be used to determine how organisms decide to choose a particular area for breeding and daily activities, which is generally poorly understood yet is of great consequence to accurately predict population survival and persistence (Pettifor et al. 2000). While the most important behavioral parameters to accurately include will vary based on the model's aim (Feró et al. 2008); experimentation can reduce uncertainty in the majority of behavior-based model parameters.

In 1996 Lima and Zollner called for a union of behavioral and landscape ecology with the aim of improving ecological modeling. Many ecologists have undertaken this challenge, increasing the number of behavioral experiments at landscape scales. Further, many ecologists agree that behavioral information should be included in predictive models (e.g., Roitberg and Mangel 1997, Vos et al. 2001, Morales and Ellner 2002, Heinz and Strand 2006, Heinz et al. 2006). Nonetheless, I argue that this growing body of literature remains underused and potentially incorrectly used in models predicting how land-use and climate change will influence species' distributions. To this end, I summarize the methods and results of research using direct experimental manipulation techniques to examine the trade-offs associated with how species respond behaviorally to various attributes of landscapes, highlight how these results could be quantified for use in predictive models, and suggest directions for future integrative research.

Experimental manipulations of animals' interactions with landscapes

Experimental methods

Translocation: Animals are captured and released at varying distances from their home ranges, and various habitat features (such as barriers, gaps, or various types of matrix vegetation) are standardized between the release site and the home range (Table 2). The motivation for movement is assumed to be to return to a home range (also termed homing) or to a more suitable habitat. The most common methods for following the movements of translocated animals are direct observation, radiotelemetry, and marking and resighting or recapturing. The translocation of animals within a landscape allows the standardization and replication of distances traveled, habitat and landscape features traversed, and motivation for movement and endpoint destinations (Belisle et al. 2001, Belisle 2005). Translocation experiments allow the determination of the distances an organism is willing or able to travel, the time required to do so, favored routes, and how the movement behavior is influenced by habitat and landscape features and configurations (Table 2, Belisle 2005). While translocation cannot fully simulate how an animal will behave in nature, it does provide an approximation of how different abiotic and biotic features influence movement behavior and the associated short-term costs (Belisle 2005). This knowledge affords more realistic quantification of the movement resistance level of habitat and matrix types in the landscape, allowing for better least-cost distance estimation, and, consequently, more accurate values for rates and patterns of dispersal. Estimates of dispersal parameters will be increasingly important for prediction of species' ability to respond to climate changes.

Playback: Used predominantly in avian research, these experiments involve playing recorded sounds of conspecifics with the aim of luring individuals out of their territories and into different habitat or matrix types or across gaps or barriers to gain information about their movement behavior (Table 2). The type of movement information obtained is similar to that of translocation experiments, but in playback experiments the motivation for movement is attraction to conspecifics; resulting from territory defense, mate attraction, predator mobbing, or distress calls (Belisle 2005). The density of both conspecifics and predators in a patch of habitat can be expected to change the quality of the patch and thus influence dispersal, either negatively or positively. Playback experiments provide a method for incorporating this influence into the quantification of dispersal. There is some question as to the ability of playback experiments to demonstrate realistic movements of birds, since their behavioral states and risk environment are altered by the playback (Sieving et al. 2000, Belisle et al. 2001). For example, birds may be more susceptible to predation during playback and thus move with greater caution. Alternatively they may be in a heightened aggressive state and thus move with less caution (Sieving et al. 2000). However, the general consensus is that playback does not misrepresent birds' behavioral limitations or decision rules (Sieving et al. 2000).

Alteration of landscapes: A labor-intensive but instructive method for determining how animals move within landscapes is the direct alteration of these landscapes (Andreassen et al. 1996a, Collinge 2000, Levey et al. 2005). This type of study involves the creation of standardized landscape features; such as numbers, distances, and sizes of habitat patches, various matrix types, or corridors of varying widths, lengths and composition. Animals are then monitored in these new landscapes to examine changes in their movement and other behaviors. Although most easily done at small scales involving insects, large landscape-scale manipulations are growing in popularity and are yielding interesting and relevant results (Laurance et al. 2002, Tewksbury et al. 2002, Levey et al. 2005, Burns and Grear 2008). Landscape manipulations can provide specific information on habitat permeability, route choice, perceptual range (sensu Lima and Zollner 1996), home range size, and maximum dispersal distance—all of which can be used to quantify dispersal carrying capacities (Table 2).

Food resource manipulation: Experiments that directly manipulate the availability of food resources can provide estimates of how foraging and movement behavior differs depending on landscape and habitat context. Controlled experiments pinpoint which factors have an influence on foraging behavior (e.g., perceived predation risk, competition, distance to human settlement, etc). Specifically, the information that can be quantified includes perceptual range, perceived predation risk, search strategies, energy reserves, resource distribution and availability, and habitat preferences (Table 2).

Reproductive success manipulation: Determining how landscape context affects reproductive success is important to evaluate species' long-term persistence (Andren 1992). The pairing success of both males and females can be influenced by a number of factors, including individual quality, territory quality, and conspecific densities (Bayne and Hobson 2001). Direct manipulation of pairing success, nest location, or reproductive success in different habitat types provides a relatively rapid assessment of these factors, allowing for the quantification of behavioral processes such as search strategies for mates, defense and size of territories, habitat preferences for mate selection and nesting, and demographic information.

Perceived predation risk manipulation: Experiments involving the manipulation of animals' perceived predation risk often involve evaluating responses to real or artificial predators, olfactory cues, or measures of predation-avoidance behaviors (e.g., scanning or hiding) to determine the levels of perceived predation risk and animals' responses in various habitat contexts (Table 2). These experiments measure how the perception of predation risk influences foraging or other behaviors, which ultimately determine how an animal uses and moves within an area. Using these methods can allow for the quantification of perceptual ranges, habitat preferences, movement alterations and travel speeds through habitat types with different predation risk (Lima and Zollner 1996).

While this review is aimed at showing applications of experimental studies to predicting how organisms will respond to altered landscapes due to climate change or human development, many types of non-experimental research can also yield similar predictive information. For example, mark-recapture studies can lead to accurate estimates of dispersal parameters (e.g., Hanski et al. 2000). However, it is beyond the scope of this paper to review the results and applications of observational studies as well. I instead stress how new, experimental methods in behavioral landscape ecology can be extremely useful for quantifying behavioral processes for use in models predicting how species will respond to land-use and climate change.

Behavioral Decisions Affecting Movement/Dispersal

Movement and dispersal are the key processes underlying the concept of landscape connectivity (Baguette and Van Dyck 2007), and usually have major affects on population viability (Fahrig 2002, Stevens et al. 2004). The degree of connectedness of a landscape depends on a great number of individual-specific traits, including: ability to cross borders between vegetation types, perceptual range, ability to move through non-habitat or matrix vegetation, and ability to cross gaps in vegetation (Bowler and Benton 2005, Stevens et al. 2006). The effects of fragmentation and human disturbance on landscape connectivity for particular individuals depends on a range of factors beyond these individual traits; such as the spatial scale over which the fragmentation or disturbance took place, the new configuration and composition of the landscape, and how drastic and over what time scale the changes occurred. An important point is that movement and dispersal can vary greatly in the same individual in different landscapes and even between individuals in the same landscape (Baguette and Van Dyck 2007); meaning that despite the extra effort required experiments and models should focus at the individual level. Once these traits are determined for individuals in a landscape, the costs (such as speed of movement, mortality, resource availability and so on) associated with the movement and dispersal patterns of the population as a whole (in the same landscape) can be more accurately determined (Stevens et al. 2006, Baguette and Van Dyck 2007). These projected costs can then be incorporated into metapopulation or individual-based models to greatly improve model predictions of how the species will respond to specific landscape change scenarios due to fragmentation or climate change. For instance, experiments which document how individuals' movement behavior is affected after deliberate fragmentation of their habitat can help to remove possible confounding variables present in many opportunistic studies, such as time since fragmentation (Table 3).

In a patchy or fragmented landscape the first decision an individual must make in order to disperse or move long distances is to cross the boundary between the suitable habitat and the matrix—this crossing probability is termed boundary permeability (Table 2, Stevens et al. 2006, Baguette and Van Dyck 2007). In fragmented landscapes, individuals that respond to these boundaries may be especially affected by landscape composition and configuration when the matrix vegetation is heterogeneous (Bender and Fahrig 2005). Further, experiments show that individuals emigrate more readily when the surrounding environment is less resistant to movement; when boundary permeability is high (Table 3, Stamps et al. 1987, Haddad 1999a). Even movement patterns within a habitat patch are often based on the matrix characteristics of the surrounding landscape (Wiens et al. 1997), and experiments show that patches and corridors surrounded by a low-contrast matrix are more readily utilized than those surrounded by a high-contrast matrix (Table 3).

The next step an individual must take to successfully disperse or move long distances in a patchy or fragmented landscape after crossing a vegetation border is to move through the matrix. The degree to which a matrix (or habitat) type impedes movement of an organism is called patch resistance or viscosity (With 1994, Wiens et al. 1997, Stevens et al. 2006). The difference between the perceptual range of the organism and the scale of spatial heterogeneity in the landscape (termed "grain size") can be critical in determining the level of resistance of landscape elements to an organism (Baguette and Van Dyck 2007). For instance, whether or not an organism homes successfully (a surrogate for movement ability) likely depends on the grain size of the landscape for that organism (Lima and Zollner 1996). Few animals' perceptual ranges are known, and more studies aimed at determining this information for a variety of taxa could help greatly in predicting species' distributions and responses to landscape and climate change (Lima and Zollner 1996). For example, in an individual-based simulation of the dispersal affects of three perceptual ranges (low, medium and high), Vuilleumier and Perrin (2006) found that when energy reserves are low a high perceptual range yields the greatest dispersal success; at intermediate reserve levels an intermediate perceptual range is best; and at high energy levels a low perceptual range yields the greatest success. In other words, if dispersal costs are high (often in highly fragmented landscapes) a high perceptual range will yield the greatest benefits; while if costs are low (continuous landscapes) and the individual has plenty of resource access, there is no need to disperse very far and a low perceptual range is suitable. Environmental cues such as temperature, moisture level, elevation changes, wind speed and direction, scent, auditory and magnetic fields are often overlooked in experiments attempting to determine the affect of landscape structure on movement ability (Stevens et al. 2006). For example, animals frequently use wind to orient toward a favored habitat—which can complicate estimates of perceptual range and permeability of various matrix types (Schooley and Wiens 2003). Determining the effect of environmental variables on animals' responses to landscapes can be important to improve estimations of both spatial and temporal variation in habitat permeability and perceptual ranges. Such information might be particularly important with weather perturbations (i.e., increased storm frequency, earlier spring warming) predicted as a result of climate change.

Animals' movement ability often varies between familiar and unfamiliar (or preferred and matrix) vegetation types (Table 3, Doncaster et al. 2001, Goodwin and Fahrig 2002, Desouhant et al. 2003, Hein et al. 2003, Bowler and Benton 2005). One prediction that has some empirical support but requires further testing is that generalists will show greater ease of movement and homing success in unfamiliar vegetation types than specialists (Table 3). Further, experiments show that the search behavior of animals in unfamiliar habitat (matrix) is often directional, as is predicted by optimal search behavior simulation models (Zollner and Lima 1999a; Schooley and Wiens 2003)—while movements within a favored habitat are usually less directional (Table 3). Thus, animals often move more quickly through non-habitat than their preferred habitat. This makes sense since dispersing individuals often suffer higher mortality rates than do non-dispersers (Baguette and Van Dyck 2007). Moving more directly (and thus more quickly) through inhospitable areas may be an evolutionary strategy to reduce the risk of mortality in these areas; while exploratory movements in suitable habitat yield greater benefits in that context (Zollner and Lima 1999a, Schtickzelle et al. 2007).

Many animals try to avoid moving through unfamiliar habitat altogether, and will often take substantial detours through preferred habitat type rather than cross gaps in that habitat type, or will choose the smallest gap available to cross (Table 3). Whether an animal moves directionally or chooses a more circuitous route to avoid all unfamiliar vegetation may ultimately depend not only on the habitat or matrix structure and associated predation risk, but its motivation and physiological limitations. For instance, one ubiquitous feature of human-altered landscapes is extensive road networks, and many animals are averse to crossing paved roads, irrespective of traffic level (Table 3). However, willingness to cross roads can vary based on the individual's motivation at the time. For example, some disturbance sensitive tropical bird species would not cross roads when the motivation was response to conspecifics (playback; Develey and Stouffer 2001); while others did cross highways easily when the motivation was to return to a home range (translocation; Laurance and Gomez 2005). This suggests that, for these birds, the motivation of return to a home range (Laurance and Gomez 2005) is stronger than response to conspecifics (Develey and Stouffer 2001). Although a willingness to cross roads will increase landscape connectivity for most species, this behavior may also cause greater mortality (e.g., Hels and Buchwald 2001). Greater mortality at road crossings is often ignored in models, and could have a significant effect on total dispersal mortality.

Since species are often averse to crossing gaps in familiar vegetation, corridors of vegetation similar to that of preferred habitat are thought to aid in the movement of animals between suitable habitat patches. Large and small-scale tests of this prediction show that many animals will readily use corridors in the landscapes to facilitate movement, while others will not (Table 3, Haddad and Baum 1999, Tewksbury et al. 2002, Haddad et al. 2003, Haddad and Tewksbury 2005, Levey et al. 2005, Townsend and Levey 2005). Short, narrow corridors can be useful for facilitating movement between suitable habitat patches, but usually are not suitable for other activities such as foraging or breeding (St Clair et al. 1998, Sieving et al. 2000). However, several studies found that predators can learn to hone in on corridors as easy places in which to ambush prey species that use the corridors for regular movement (Bekker and Canters 1997, Brinkerhoff et al. 2005). Differences in findings on the efficacy of corridors for enhancing movement between suitable habitat patches may, in part, be due to differences in experimental design (i.e., whether or not changes in area and shape were controlled for (Haddad and Baum 1999, Tewksbury et al. 2002), and the particular species studied (Tewksbury et al. 2002). However, given the findings above, I think it is safe to say that corridors do confer a large benefit to most species in most landscapes in terms of increasing landscape connectivity—although species and landscape-specific experiments should be done before incorporating the results into predictive models. For instance, studies combining observations and experiments might help uncover other factors which determine the ultimate affect of corridors on populations and species—such as density dependant dispersal or alteration of predator behavior (Bekker and Canters 1997). Research on how corridors influence animal movement is critical for reserve design in the face of climate change. Given the omnipresence of human-modified landscapes, many species will not be able to avoid moving through various types of matrix vegetation as they track the changing climate. If species cannot readily move through human-modified landscapes corridors may provide a viable solution allowing organisms to track their climate envelopes (Hannah et al. 2002, Hellmann et al. 2008). The extensive work done on the effectiveness of corridors to date will be extremely useful to begin to evaluate if this mitigation method will be effective.

Empirical tests demonstrate that translocated animals often exhibit different movement behavior than conspecific residents (Table 3). These findings are most applicable to conservation situations in which a resident population must be moved in order to avoid destruction and illustrate that relocated animals must expend more energy than residents, which can produce delayed or deferred costs (Zollner and Lima 1999a, Stamps et al. 2005a). However, there is some evidence that suggests that after settling immigrants may have higher fitness than residents (Baguette and Van Dyck 2007). Behavioral results from translocation experiments should provide valuable insight on the probability of success of assisted migration—a somewhat controversial management strategy whereby animals are moved to more favorable climates as their customary ranges undergo climate change (Hunter 2007, McLachlan et al. 2007, Hoegh-Guldberg et al. 2008).

Interestingly, there appears to be no clear patterns with regard to differences in intraspecific male and female movement abilities. Whether differences in the movement behavior of each sex are observed likely depends on the mating and parental care system of the species, as well as the other factors mentioned above. Age also likely plays a role in movement ability, although experimental studies testing this idea are lacking (but see Collins and Barrett 1997, Rothermel and Semlitsch 2002, Rothermel 2004, Stevens et al. 2004, Stevens et al. 2006). Age related movement is especially important for determining juvenile dispersal ability; conducting translocation or other movement experiments on adults may yield an inaccurate picture of the dispersal patterns of the individuals in a population.

Biotic factors are another commonly overlooked influence on animals' movement behavior. Biotic factors can include con-specifics, predators, competitors, food resources, or even the physiology of the animal. For example, while body size is the only physiological variable that has been examined in behavioral landscape ecology experiments; however, other physiological attributes may affect how an organism responds to landscapes. Further, the density of conspecifics, competitors and predators surely influences movement and dispersal decisions, but experimental results are lacking (Turchin 1998). Direct experimental results regarding how well an individual moves across boundaries and through various habitat and matrix types are essential to creating realistic dispersal rate functions in spatially explicit models (Desrochers et al. 1999, Belisle 2005). Determining the directionality, speed of movement and willingness to move through various vegetation types allows for more detailed quantification of the associated resistance levels for the species in landscapes with various habitat compositions and configurations. This information can be especially important in predicting how an organism will respond to translocation to a novel area or alteration of its native region due to human-use or climate change.

Behavioral Decisions Influencing Habitat Selection and Reproductive Success

After an animal has successfully dispersed to a new area, it must decide where to stay to attract a mate and attempt to reproduce. Determining how an animal selects this area is essential to predicting its long term persistence, due to the different costs associated with the selection. Thus far, the range of experimental manipulations aiming to determine the behavioral decisions that influence habitat selection and reproductive success is less diverse than those focusing on movement and dispersal. Nonetheless, these experiments yield critical insights into how individuals' behavior influences species' persistence in changing landscapes (Fig. 1). One focus of this type of experimental work is to identify how conspecific and heterospecific attraction influence habitat choice, using playback experiments and manipulations of conspecific and heterospecific densities. Playback experiments to date have focused mainly on birds, where researchers have determined that attraction to conspecifics often determines where a bird chooses to set up its territory. In these experiments researchers broadcast territorial calls of the target species in plots previously unoccupied by that species, sometimes in both optimal and sub-optimal habitat or in patches of varying sizes, and compare settlement rate with control plots. Many territorial songbirds responded to playback of conspecific vocalizations by settling in the playback area, even in sub-optimal or small patches of habitat, and often fledged young and returned to the same site in the following years (Table 4, Ward and Schlossberg 2004, Ahlering et al. 2006, Nocera et al. 2006, Hahn and Silverman 2007, Fletcher and Hutto 2008, Fletcher 2007, 2009). However, since Hahn and Silverman (2006) found that variation did exist in the age of the birds that chose to settle, it is very likely that the effect of conspecific attraction differs by age, experience and arrival timing. Still, this type of knowledge will be extremely helpful in motivating birds to settle in newly created suitable areas or areas that have been previously unoccupied for other reasons (Ahlering and Faaborg 2006). Other conspecific or heterospecific cues can also help to determine where birds choose to set up territories, such as high parental feeding rates (Part and Doligez 2003) or reproductive success in previous years (Haas 1998).

Manipulations of conspecific and heterospecific densities involve presenting individuals with a choice of patches containing similar food resources but differing in the presence or density of conspecifics or heterospecifics. Results of these experiments show that these cues are important for habitat selection not only in birds but across multiple taxonomic groups (Table 4, Hodge and Storferlsser 1997, Monkkonen et al. 1997, Stamps 1988, Forsman et al. 2002, Thomson et al. 2003, Stamps et al. 2005b, Parejo et al. 2008, Forsman et al. 2009). For example, flies, crabs and lizards all chose patches with a high density of conspecifics significantly more often than those without (Stamps 1988, Stamps et al. 2005b). However, the relative importance of conspecific and heterospecific cues is inconsistent across species. For instance, in voles (*Microtus ochrogaster and M. pennsylvanicus*) conspecific attraction positively influenced immigration to a patch whereas heterospecific attraction had no affect (McGuire et al. 2009). Conversely, in migratory birds heterospecific attraction was very important for habitat selection (Monkkonen et al. 1997, Forsman et al. 2002, Thomson et al. 2003, Forsman et al. 2009). Nonetheless, both conspecific and heterospecific attraction can now be recognized as having great potential to produce large scale influences on species' distributions and sensitivities to fragmentation (Fletcher 2009), and predictive models incorporating empirically derived estimates of this attraction will greatly aid in increasing the accuracy of these models in changing landscapes.

Further biotic influences on habitat selection of a species in different landscapes are availability and spatial distribution of both food resources and predators. The amount of food remaining in a patch after an individual quits foraging (termed the giving-up density or GUD) can be used as an indicator of the forager's perception of predation risk and the cost vs. gain of foraging (Brown 1988, Shochat et al. 2004). Experiments in behavioral landscape ecology sometimes use measures of GUD at artificial food patches placed in various parts of the landscape to examine how attributes of habitats and landscapes influence foraging behavior and, in turn, species' spatial distributions (Belisle 2005). Several of these experiments in urban areas suggest that to live in urban environments animals need to be more efficient at consuming food than those in natural environments, most likely due to the increased risk of predation in urban environments (Shochat et al. 2004). Further, for urban species, there seems to be a balance between the use of human presence as a cue for food and avoidance of humans as potential predators (Fernandez-Juricic et al. 2001). In experiments in natural and fragmented habitats, GUDs were higher under greater perceived predation risk (i.e., areas that are more open, illuminated, or with predator cues; Table 4). Some species did not alter their GUDs in the presences of native, recently introduced, or non-native predators; but did alter it under different microhabitat conditions—thus, indirect cues were more important than direct cues in the assessment of predation risk for these species (Table 4, Pusenius and Ostfeld 2002, Orrock et al. 2004).

Experiments employing artificial predators, trained live predators, or olfactory predator cues found that prey animals change their foraging (or other behavior) and location under greater levels of perceived predation risk (Table 4). Increased perceived predation risk can also change competitive interactions (Abramsky et al. 1998, Abramsky et al. 2004). For instance, in the presence of a trained predator, competition between two gerbil species was negated, although intraspecific competition remained (Abramsky et al. 1998, Abramsky et al. 2004). These results illustrate the large affect predators have on the spatial distribution and foraging efficiencies of prey species. Novel or introduced predators often infiltrate human-altered landscapes with ease, and can have especially detrimental effects on native prey species. Predictive models should take into consideration the abundance and distribution of predators in the study area to more accurately model the behavior of focal prey species (in individual-based models) or to predict habitat use and its costs.

To further examine the effects of habitat degradation on prey species, researchers placed feeding stations in open areas at various distances from forest edge and found that for forest birds, risk-taking in the form of venturing into more open areas increases when food is scarce and decreases at increasing distances from forest edges (Table 4, Desrochers et al. 2002, Turcotte and Desrochers 2003). Recorded playbacks of mobbing calls (used by birds to chase away predators) increased the rate of visits to feeders located less than 10 meters from forest edge, but decreased the visits of those located 10 or more meters from the edges; while a fake predator placed near a feeder caused birds to almost never visit that feeder (Desrochers et al. 2002). Forest birds weigh the risk vs. benefit of obtaining food outside of forest cover, and thus the spatial distribution of food in disturbed landscapes likely has a large impact on the survival of many forest-dwelling prey species. For instance, predation rate on ruffed grouse (*Bonasa umbellus*; Yoder et al. 2004) and red squirrels (*T. hudsonicus*; Kenward and Hodder 1998) increases in unfamiliar space vs. familiar space. Models should include information on whether time spent in matrix vegetation increases the risk of mortality, and how this is likely to affect behavioral decisions and access to food resources.

Few studies thus far have examined how habitat selection at landscape scales influences pairing success (Bayne and Hobson 2001). However, work with ovenbirds (*S. aurocapillus*) has shown that landscape factors such as fragment size, distance of the territory from an edge, anthropogenic noise level, and amount of forest cover surrounding fragments influences pairing success of territorial male ovenbirds (Table 4, Villard et al. 1993, Van Horn et al. 1995, Bayne and Hobson 2001, Habib et al. 2007). Direct removal experiments of territorial males demonstrated that floaters (wandering non-territory holding males) did exist and quickly took over the vacant territory sites in continuous forest, but these floaters rarely occurred in fragments created by agriculture (Bayne and Hobson 2001). Further, females chose to pair with males much more frequently in continuous forest than in fragments surrounded by agriculture or forestry, and males with territories closer to edges were less likely to successfully pair than those in forest interiors (Table 4, Bayne and Hobson 2001). Conversely, female brown treecreepers (*Climacteris picumnus*) translocated to unpaired males in fragmented and contiguous habitats paired equally well in both situations—leading the authors to conclude that limited female dispersal ability was the reason for the observed lack of pairs in isolated forest fragments (Cooper and Walters 2002). Manipulating nest site location is another way to gain understanding about how attributes of landscapes affect reproductive success (Belisle 2005). For example, Huhta et al. (1999) found that nestlings of pied flycatchers (*Ficedula hypoleuca*) in nests that had been moved to edge habitat had lower body mass than nests moved to interior habitat. Further, indigo buntings (*Passerina cyanea*) began preferentially nesting in edges after the fragmentation of their habitat, which lead to lowered overall nesting success (Table 4, Weldon and Haddad 2005). Birds also chose to nest more frequently and sang more vigorously in areas with experimentally decreased predator abundances than in control sites, although settlement and breeding phenology were not affected (Fontaine and Martin 2006a). In areas with decreased predation parents invested more in their young (increased egg size, clutch mass and rates of feeding), males increased feeding of incubating females, and females spent less time incubating (Table 4, Fontaine and Martin 2006b). Experiments which manipulate conditions for pairing and reproducing will allow models to more accurately predict the affects of landscapes on habitat choice and demography.

Conclusions and future directions

Behavioral landscape ecology provides a strong theoretical framework for predicting the costs and benefits associated with how individuals move or disperse through the landscape, choose habitat in which to settle, and produce offspring which survive to repeat the process. Recently, empirical results combined with models have been used to test these predictions (Lima and Zollner 1996, Macdonald and Rushton 2003, Belisle 2005, Stevens and Baguette 2008). These models include populations or individuals, the heterogeneous vegetation types within a landscape, and the interactions between them; and when parameterized with sufficient and accurate information can be essential in conservation planning and predicting species' responses to climate change (Zollner and Lima 2005, Russell et al. 2007). To create models with a theoretical cost-benefit framework requires information on species' behaviors and landscape characteristics. These additional variables needed to accommodate this framework may lead to more complex models, which some may argue is undesirable (e.g., Minor et al. 2008). However, I suggest that in many cases added complexity will allow the research to be placed in a theoretical context which will allow for better understanding of the mechanisms driving the observed patterns and will improve predictability into the future and thus conservation planning. Nonetheless, it is important to understand the problems that can arise in models with many variables and to examine different ways to deal with uncertainty. Thus, I believe that predictive, spatially explicit models using quantification of the results of experimental studies such as the ones reviewed in this paper should be recognized as having great potential for informing critical management decisions.

Although to date few researchers have used the results of experiments in behavioral landscape ecology to inform models for conservation planning, the following two examples illustrate the potential utility of this approach and how it can be accomplished. Firstly, Castellón and Sieving (2007) examined how Chucao Tapaculos (*Scelorchilus rubecula*) responded to patch boundaries using song playback experiments (Sieving et al. 1996) and the degree of permeability of different landscape elements using translocation experiments (Castellón and Sieving 2006). They then used this and other empirically derived information on daily movement rates, territory sizes, survival, etc. to parameterize population viability, patch occupancy and graph theoretical models to predict numbers of breeding territories that could be accommodated within patch configurations and to evaluate the potential affect of placing corridors in the landscape (Castellón and Sieving 2007). They found that adding corridors to a landscape with an intermediate fragmentation level would likely quadruple the Chucao population and might prevent the extinction of another species; demonstrating how useful this approach can be for conservation planning (Castellón and Sieving 2007). In a second example, Stevens and colleagues (2006a) used translocation experiments to determine boundary permeabilities and resistance levels of different landscape elements for Natterjack toads (*Bufo calamita*) (Stevens et al. 2004, Stevens et al. 2006b). They then used these behavioral results to parameterize a model of the toads' dispersal using cost-distance modeling and produced an estimate of the functional connectivity of the landscape, which they validated using a landscape genetics approach (Stevens et al. 2006a). This combination of methods allowed the researchers to inform conservation planners of the need for forested corridors between toad populations in the landscape—a result which was not expected a priori (Stevens et al. 2006a).

The application of experimental research in behavioral landscape ecology to long-term predictions of species' persistence is just beginning to receive recognition, and yet these and other interesting results have already emerged (Tables 3 and 4). Further, the conclusions from these findings are often generalizable across the diverse range of taxa studied, and highlight the trade-offs faced by these organisms. For instance, the experiments on movement and dispersal ability clearly illustrate the trade-off between dispersal and mortality risk, in that: 1) movement was usually faster and more directional in unfamiliar or sub-optimal areas; 2) substantial detours were often taken through preferred habitat to avoid gaps in that habitat; 3) movement appeared to be augmented for most taxa when corridors were present in a given landscape; 4) movement patterns depended not only on the characteristics of the patch the animal was in, but on those of the surrounding landscape as well; 5) movement behavior and homing ability differed between habitat generalists and specialists; and 6) translocated animals often exhibited different behavior than residents. As for habitat selection, the trade-off between food or other resource availability and predation risk was especially apparent; conspecific cues were important in habitat choice and the perception of predation risk altered feeding and other behaviors. Further, reproductive success was generally lower in edge vegetation, predation perception affected reproductive effort, and pairing success often decreased in disturbed vegetation. These results allow processes within the theoretical framework of behavioral landscape ecology to be quantified, which can also guide model parameterization when experimental validation is not possible.

Still, much information useful for predicting how animals will respond to new landscapes can be gained from further experiments in behavioral landscape ecology. In terms of the costs and benefits of movement and dispersal, areas that need further examination include: 1) the effect of natal vegetation type on differences in intraspecific movement ability; 2) the effect of border types and matrix contrast on behavioral decisions; and 3) the effect of roads on both the behavior and mortality of organisms. Research areas of particular importance regarding habitat selection include: 1) the strength of conspecific cues in habitat selection; 2) the effect of perceived predation risk on behavioral decisions; and 3) how conspecific densities affect behavioral decisions. Finally, the effect of landscape composition and configuration on the costs and benefits of all stages of reproduction—from territory establishment, mate attraction and rearing of young—needs more attention. Traits such as perceptual range can be difficult to estimate. However, experiments yielding this information can greatly decrease model uncertainty regarding how an animal is able to move through various landscape types, including gap-crossing ability. Further, the affect of environmental variables on animal responses to landscapes deserves more attention, as do physiological variables such as body size or color (e.g., Wunder and Norris 2008). Another promising method for determining the costs and benefits of individual's decisions in varying landscapes is landscape genetics (Stevens et al. 2006, Stevens and Baguette 2008). While this topic is beyond the scope of this review, landscape genetics provides a way to combine experiments on movement and habitat selection behavior with dispersal information obtained via gene flow estimates at landscape scales to understand the functional connectivity of a landscape for a particular species (Stevens et al. 2006).

A central goal of conservation biology is to prioritize species and regions for protection from endangerment and extinction (Brummitt and Lughadha 2003). Increasingly, conservation biologists are also taxed with managing landscapes and species of conservation concern in the face of climate change. Addressing these conservation challenges requires knowledge of species' distributions and abundances at relevant spatial scales, and predictions of how those distributions and abundances are likely to change in the future (Davies et al. 2000). Species distributions depend on complex interactions between trade-offs associated with individual behaviors and the landscape composition and configuration (Lima and Zollner 1996, Sutherland 1998). As this paper highlights, there is great potential for interesting and relevant results to emerge from experiments in behavioral landscape ecology. It is my hope that researchers will not only undertake these experiments, but will increase their collaborations with ecological modelers and theoretical biologists to create robust models of species' responses to dynamic landscape conditions. This research agenda is critical for protecting animal populations under current and impending land-use and climate changes.

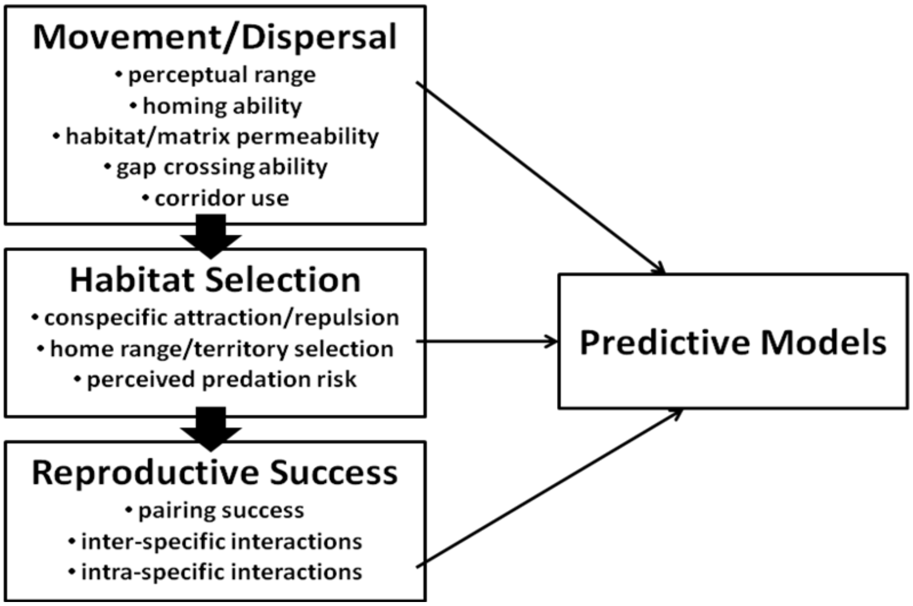

Figure 1. The three main steps individuals and species must complete in order to persist and the important traits or behaviors involved at each step. Landscape-level experiments can be used to obtain behavioral information. Predictive models incorporating these traits and behaviors will give more reliable predictions of species' responses to climate and land-use change.

Table 1. Landscape ecology terms and how they are defined in this paper.

Term	Definition
Landscape	Regional scale; an area often consisting of a mosaic of different biotic and abiotic features with a common climate or geomorphology
Habitat	Local scale; population specific—any part of the landscape a population uses for survival or reproduction (as opposed to just passing through)
Matrix	Local scale; population specific—any part of the landscape a population does not use for survival or reproduction
Landscape Composition	The different biotic and abiotic features within the landscape that often correspond to phytosociological or physionomical elements
Landscape Configuration	The spatial arrangement of the different biotic and abiotic features within the landscape

Table 2. Behavioral measures or traits that can be quantified for later use in predictive models and the experiments used to determine them.

Behavior/Trait	Definition	Relevant Experiment	Quantification Example
Perceptual Range	Distance at which objects (such as habitat) can be detected	Deliberate alteration of habitat; translocation	Create a buffer (probability boundary) in which a species can detect a target object
Homing Ability	The species' ability to return to their home range	Translocation	Help define maximum dispersal distances and least-cost movement pathways
Habitat or Matrix Permeability	In highly permeable areas the animal shows little hesitation and moves easily	Deliberate alteration of habitat; translocation; playback	Define resistance or friction level of an area and define least-cost pathways
Habitat Selection	Occurs when an organism can detect boundaries between different areas and chooses one over the other	Deliberate alteration of habitat; translocation; playback; density manipulations	Change the attractiveness level of different patches of vegetation and help define boundary permeabilities
Gap Crossing Ability	The species' ability/willingness to traverse stretches of matrix vegetation or clearcuts	Translocation; playback	Aid in defining least-cost pathways and dispersal abilities
Corridor Use	Ability/willingness of a species to travel through a narrow stretch of habitat or matrix vegetation that connects habitat	Deliberate alteration of habitat; translocation	Define least-cost pathways and dispersal abilities in varying landscapes
Con/Heterospecific Attraction/Repulsion	Alteration of movement behavior when members of the same species are detected	Playback; density manipulations	Change the attractiveness level of a patch of vegetation and can influence reproductive success
Pairing Success	Ability of individuals to locate and mate with a conspecific	Translocation	
Perceived Predation Risk	An animals' sense of danger from predators	Feeding stations; playback; predator cue manipulation	Change the attractiveness level of different vegetation types

Table 3. A representative summary of the experimental methods, observed behaviors, factors influencing the responses, possible costs and benefits and study organisms used in behavioral landscape ecology experiments examining movement and dispersal ability.

Experiment	Observed Behavior	Factors Influencing Response	Possible Costs	Possible Benefits	Study Organisms	References
Deliberate fragmentation of individuals' habitat	One or more of the following: decreased home range size; greater territory overlap; longer dispersal distances; greater rates of emigration	Perceptual range; gap crossing ability; matrix vegetation crossing ability; time and spatial scale of fragmentation; boundary permeability	Decreased movement and dispersal ability due to inability to cross gaps or matrix vegetation; increased mortality during dispersal due to longer dispersal distances; reduction of usable habitat leading to overcrowding and depletion of resources	Selection for faster dispersal or no dispersal due to the increased risk of mortality over the longer dispersal distances required or through gaps or matrix vegetation	Tropical forest fauna; root, meadow and field voles; white-footed mice; butterflies; salamanders; frogs and toads	Collins and Barrett 1997; Andreassen and Ims 1998, 2001; Laurance et al. 2002; Evans et al. 2006; Aviron et al. 2007; Burns and Grear 2008; Semlitsch et al. 2008
Translocation away from home range to determine ability to return through matrix vegetation	Decreased homing success with increasing translocation distance	Perceptual range; gap crossing ability; matrix vegetation crossing ability; boundary permeability	May not attempt movement far from home range, meaning overcrowding in nearby habitat and depletion of resources	May not attempt movement far from home range, meaning lower mortality rates due to decreased dispersal distances	Colorado potato beetles; red-backed salamanders; edible frogs; gray squirrels	Follett et al. 1996; Goheen et al. 2003; Marsh et al. 2004; Mazerolle and Vos 2006
Translocation away from home range to determine movement ability and speed in unfamiliar areas	More directional (and thus faster) movement in unfamiliar areas	Type of vegetation; boundary permeability; perceptual range	Greater energy requirement with faster movement speeds; greater risk of starvation if suitable habitat is not located; may bypass resources along the way due to lack of slower, exploratory movements	Lower risk of predation in unfamiliar areas due to increased speed of movement; lower risk of starvation if suitable habitat is located quickly	Cactus bugs; goldenrod beetles; tenebrionid beetles; damselflies; crickets; rice rats; butterflies; red squirrels; edible dormice; hedgehogs; box turtles	Crist et al. 1992; Wiens et al. 1997; Bright 1998; Pither and Taylor 1998; With et al. 1999; Doncaster et al. 2001; Goodwin and Fahrig 2002; Schooley and Wiens 2003; Schooley and Branch 2005; Bakker 2006; Rittenhouse et al. 2007; Schtickzelle et al. 2007

Road-crossing motivation given via translocation away from home range or playback of conspecifics	Inability to cross roads	One or more of the following: traffic or noise level; road substrate; gap in vegetation; olfactory cues; low boundary permeability	Inability to disperse if crossing a road is necessary	Lower traffic-induced mortality rates due to unwillingness/inability to cross roads	Mice; chipmunks; small snakes; tropical forest birds	Develey and Stouffer 2001; Andrews and Gibbons 2005; McGregor et al. 2008
Translocation to an area of experimental habitat patches	Preference for patches with high boundary permeability (i.e. those surrounded by a low contrast matrix)	The boundary permeability of the habitat patch; perceptual range	Inability to use, emigrate to or immigrate from good patches with low boundary permeability (surrounded by high contrast matrix)	There may be lower predation risk and other edge effects in patches with high boundary permeability, meaning choosing them could be beneficial	Beetles; house flies; planthoppers	Wiens et al. 1997; Collinge and Palmer 2002; Haynes and Cronin 2003; Fried et al. 2005
Translocation away from home range across vegetation gaps to determine ability to return and route choice	Long detours through vegetation taken to avoid crossing a gap; or chose to cross smallest gap available	Gap distance; perceptual range; type of detour vegetation and distance; perceived predation risk; motivation given	Greater energy requirement when detour is taken; unwillingness to disperse to good habitat if it requires crossing a large gap	Lower risk of predation if gap is avoided or smaller gap chosen	Forest birds; edible dormice; red squirrels; root voles; red-legged frogs; natterjack toads; Florida scrub lizards; damselflies	Andreassen et al. 1996b; Desrochers and Hannon, 1997; Rail et al. 1997; Bright, 1998; St Clair 1998; Hokit et al. 1999; Jonsen and Taylor 2000; Belisle and Desrochers 2002; Chan-McLeod 2003; Bakker and Van Vuren 2004; Bosschieter and Goedhart 2005; Laurance and Gomez 2005; Castellon and Sieving 2006; Huste et al. 2006; Tomasevic and Estades 2008
Creation of a landscape with corridors connecting habitat patches	Corridors were used to travel to habitat patches	Intervening matrix type; boundary permeability; perceptual range; corridor dimensions	Greater risk of predation in corridors if predators learn the route	Ability to disperse to good habitat if a corridor is available	Butterflies; mice; seed-dispersing birds; root voles; house flies; forest birds;	Andreassen et al. 1996a; Andreassen et al. 1998; St Clair et al. 1998; Aars and Ims 1999; Aars et al. 1999; Haddad and Baum 1999; Haddad 1999a, 1999b; Haddad 2000; Sieving et al. 2000; Andreassen and Ims 2001; Dover and Fry 2001; Tewksbury et al. 2002; Haddad et al. 2003; Fried et al. 2005; Haddad and Tewksbury 2005;

						Levey et al. 2005; Townsend and Levey 2005
Translocation of habitat generalists and specialists to determine differences in homing or movement ability	Generalist species moved more readily through unfamiliar areas than did specialists	Specialist level of the species	Greater risk of predation and starvation for generalists if they are unable to find suitable habitat; specialists may become overcrowded if unable to disperse to unfamiliar areas	Generalists may be able to locate more resources since they are willing to move through unfamiliar areas; specialists may have lower mortality rates due to predation or starvation due to unwillingness to move through unfamiliar areas	Ovenbirds; white-throated sparrows; eastern chipmunks; white-footed mice; leopard frogs; southern toads; marbled salamanders; butterflies	Desrochers and Hannon 1997; Rail et al. 1997; St Clair et al. 1998; Haddad 1999b; Gobeil and Villard 2002; Hannon and Schmiegelow 2002; Bender and Fahrig 2005; Graeter et al. 2008
Translocation of intraspecific males and females to determine differences in homing or movement ability	No difference in movement behavior or distance between the sexes	Mating and parental care system; spatial and temporal scale; intervening matrix type	Greater risk of inbreeding if both sexes are unwilling to disperse	Increased ability to find a mate if both sexes show similar movement or dispersal tendencies	Damselflies; red, gray and fox squirrels; eastern chipmunks; brushtail possums; flightless bush crickets; southern toads	Pither and Taylor 1998; Cowan 2001; Bowman and Fahrig 2002; Goheen et al. 2003; Diekotter et al. 2005; Graeter et al. 2008
Translocation of intraspecific juveniles and adults to determine differences in homing or movement ability	Juveniles and adults showed different homing or movement ability	Age	Juveniles may suffer greater mortality rates due to predation or starvation because they often disperse or move farther; adults may be restricted in their ability to move to better habitat	Juveniles may reach habitat with greater food or territory resources because they often disperse or move farther; adults may suffer less predation or starvation by staying put	Natterjack toads; American toads; meadow voles	Collins and Barrett 1997; Rothermel and Semlitsch 2002; Rothermel 2004; Stevens et al. 2004; Stevens et al. 2006b
Translocation in different environmental conditions to determine the effect on homing or movement ability	Movement behavior varied with weather and climate conditions	Wind speed and direction; humidity level; rain; sun intensity; visual, auditory, tactile and olfactory cues	Extreme or changing weather patterns may disrupt normal movement or dispersal ability or cause risk of mortality due to desiccation or exposure	Lower risk of mortality due to predation, desiccation or exposure when moving or dispersing if the individual only moves when conditions are favorable	Rice rats; cactus bugs; southern leopard frogs; southern toads; marbled salamanders; edible and red-legged frogs	Chan-McLeod 2003; Schooley and Wiens 2003; Schooley and Branch 2005; Mazerolle and Vos 2006

Table 4. A representative summary of the experimental methods, observed behaviors, factors influencing the responses, possible costs and benefits and study organisms used in behavioral landscape ecology experiments examining habitat selection and reproductive success.

Experiment	Observed Behavior	Factors Influencing Response	Possible Costs	Possible Benefits	Study Organisms	References
Playback of conspecifics in unoccupied habitat to determine the influence on birds' nesting site selection	Birds set up territories in previously unoccupied habitat if they heard conspecifics there	Age; experience; arrival timing; presence of conspecific cues	Habitat may become overcrowded; predation risk and food resource level unknown at time of settling	Can be an effective way to cue into suitable habitat; more potential mates available; reduced search costs	Songbirds; flycatchers	Ward and Schlossberg 2004; Ahlering et al. 2006; Ahlering and Faaborg 2006; Nocera et al. 2006; Hahn and Silverman 2007
Manipulation of con- or heterospecific densities in patches to determine the influence on patch choice	Patches with high conspecific or heterospecific densities were most often preferred	Conspecific and heterospecific densities; foraging strategy	Overcrowding; depletion of food resource; high competition for mates; resource level unknown at time of settling	More potential mates; reduced search costs	Migratory birds; voles; spiders	Stamps 1988; Hodge and Storferlsser 1997; Monkkonen et al. 1997; Forsman et al. 2002; Thomson et al. 2003; Stamps et al. 2005; Fletcher 2007; Fletcher and Hutto 2008; Parejo et al. 2008; Fletcher 2009; Forsman et al. 2009; McGuire et al. 2009
Reproductive success manipulations to determine the influence on birds' nesting site selection	Birds settled less frequently in habitat where they or conspecifics experienced lower reproductive success	Age; experience; arrival timing	Conditions may change in the following year so that birds could have experienced greater nesting success in the same area if they had chosen it again	Birds may suffer lower rates of nest failure if they can cue into conspecifics or learn from their own nest failure in areas with high predation or other risk factors	Flycatchers; robins; thrashers	Haas 1998; Part and Doligez 2003
Feeding stations placed in areas with varying cues of predation risk to determine the effect on habitat selection and feeding rates	Giving up densities (GUDs) were higher under greater levels of perceived predation risk	Perceived risk of predation; direct vs. indirect predation risk cue; energy level	Food consumption is lower under greater perceived risk of predation and thus starvation more likely	Risk of predation may be lower when GUDs are greater since animals spend less time in the open	Meadow voles; gerbils; common voles; old-field mice; fox and gray squirrels; chipmunks	Bowers et al. 1993; Kotler et al. 1993a; Kotler et al. 1993b; Jacob and Brown 2000; Schmidt 2000; Pusenius and Schmidt 2002; Orrock et al. 2004

Predation risk cues were varied to determine the effect on habitat selection	Movement, foraging and competitive behavior changed under greater perceived risk of predation	Perceived risk of predation	Normal behaviors such as mate-searching, foraging, or dispersal may be disrupted	If predation risk is high, changing behaviors may decrease mortality rate	Gerbils; old-field and cotton mice; bank and meadow voles; planthoppers; spider mites; treefrogs	Jedrzejewski et al. 1993; Kotler et al. 1993b; Abramsky et al. 1996; Abramsky et al. 1997, 1998, 2002; Grostal and Dicke 1999, 2000; Abramsky et al. 2004; Cronin et al. 2004; Rieger et al. 2004; Brinkerhoff et al. 2005; Russell et al. 2007
Feeding stations placed at varying distances to forest edge to determine the effect on forest birds' habitat use and feeding rates	Birds fed at stations more often when food was scarce or closer to forest edges; when conspecific cues were present; and under low perceived predation risk	Distance of feeding station to forest edge; food abundance; energy level; conspecific cues; perceived predation risk	Risk of starvation and predation may be greater in patchy areas since birds may be unwilling to leave cover to find food	Birds may lower their risk of predation by not venturing far from forest cover and by using conspecific cues to determine safety levels	Forest birds	Desrochers et al. 2002; Turcotte and Desrochers 2003
Translocation to or removal from fragmented or continuous habitat to determine effect on pairing success and territory settlement of forest birds	Females preferred to pair with males farther from edges and in continuous habitat; floaters occurred in continuous but not fragmented habitat	Fragment size; territory distance to edge; anthropogenic noise level; amount of forest cover	Males with territories in fragments of habitat or near edges may not be able to find a mate; males may wait to establish a territory in continuous forest rather than going to fragments	Birds who avoid pairing and nesting in fragments may have greater reproductive success	Ovenbirds	Villard et al. 1993; Van Horn et al. 1995; Bayne and Hobson 2001; Habib et al. 2007
Manipulation of forest birds' nest site location to determine effect on reproductive success	Birds with nests moved to edges suffered lower reproductive success	Distance to edge; matrix composition	Birds nesting near edges due to a lack of other sites or misleading cues will have lower reproductive success	Nesting in edge habitat may be preferable to not nesting at all if there are no other choices	Pied flycatchers; indigo buntings	Huhta et al. 1999; Weldon and Haddad 2005
Predator removal at breeding sites to determine effect on reproductive efforts of forest birds	More frequent nesting; more vigorous singing; increased parental investment in young; less time spent incubating	Presence of predators	Presence of predators decreases reproductive success even before predation attempts can be made	Decreased parental investment in reproduction may save energy in areas with high predation risk	Forest birds	Fontaine and Martin 2006a, b

Chapter 3 - Species interactions are disrupted by habitat degradation in the highly threatened Tumbesian region of Ecuador

Introduction

Human alteration of land is one of the greatest threats to species' persistence (King and With 2002, Damschen et al. 2006). While the effects of different types of human land use on species' persistence has been well studied in temperate regions, these results cannot necessarily be generalized to tropical regions, which have more complex natural landscapes and often suffer from different types of human use. For example, extensive areas of the tropics are undergoing small-scale clearing of trees and livestock grazing by rural communities, yet few studies have examined the impacts of these common activities (but see Matthysen et al. 2008). To thoroughly examine the effects of land use on species' persistence it is important to evaluate a variety of fitness surrogates, other than those that are most commonly used, namely species' abundances (Thompson 1996, Gram et al. 2003). For instance, species interactions are often ignored and yet ultimately can impact food web energy transfer and the functioning of an ecosystem (Hector and Wilby 2009, Trawell et al. 2010). Species interactions are also among the mechanisms responsible for a significant amount of evolutionary diversity, and thus any holistic conservation approach should attempt to preserve these interactions (Bonebrake et al. 2010). Mixed species associations are common across many taxa, including insects, mammals, fish and birds. In the tropics, one of the most ubiquitous interspecific interactions occurs in mixed species foraging flocks of birds. These interspecific associations allow for valuable transference of information (such as risk) across species, often at a lower cost than in intraspecific groups (Seppanen et al. 2007, Goodale et al. 2010). Further, the potential of mixed species groups to be models for community ecology has recently been recognized, and given their global ubiquity these groups offer opportunities for examining universal patterns among communities with different evolutionary histories (Goodale et al. 2010). Therefore, I believe that examining intraspecific associations across diverse communities is of the utmost importance to both answering basic theoretical questions in community ecology and for conserving species' diversity in the face of anthropogenic landscape change. In this paper I examine the impacts of rural community activities that are pervasive in tropical regions on mixed species flocks of birds in a unique coastal tropical dry forest ecosystem, with the aim of both advancing our understanding of mixed species associations and how best to conserve them.

Despite the pervasiveness of livestock grazing by rural communities in tropical regions, very few studies have quantified the effects of this activity on native fauna (but see Aerts et al. 2008, Lees and Peres 2008). Further, the majority of existing studies show that vegetation change induced by livestock grazing has negative effects on bird species richness (e.g., Aerts et al. 2008, Lees and Peres 2008), but little is known about how species interactions are impacted. The majority of tropical birds spend all or part of their foraging time in mixed species flocks, strongly suggesting that this behavior increases the fitness of these species (Maldonado-Coelho and Marini 2004, Pomara et al. 2007). Species are commonly thought to have evolved to participate in mixed flocks to gain fitness via either: 1) enhanced protection from predators due to earlier warning calls or lower probability of being singled out by a predator; or 2) greater foraging efficiency due to the flushing of insects as the flock moves through an area, kleptoparasatism, or learning new methods of food capture by watching other flock participants; or some combination of both factors (Morse 1977, Munn and Terborgh 1979, Munn 1984, Powell 1985, Terborgh et al. 1990, Jullien and Thiollay 1998). In a comprehensive study of the survival rates of birds in three categories (obligate flockers, facultative flockers, and non-flockers) in various humid forests, Jullien and Clobert (2000) found that more frequent flockers show much higher survival rates than less frequent flockers. Thus, human-induced changes that disrupt flocking behavior will likely have negative consequences on the future persistence of these species.

The Tumbesian region of south-western Ecuador and north-western Peru encompasses the great majority of remaining coastal tropical dry forest in South America, and is overlooked in terms of effects of livestock grazing on native fauna. The region has already lost over 95% of its original forest and is now one of the most threatened in the world due to heavy human use, partly in the form of extensive livestock grazing by rural communities (Best and Kessler 1995). The Tumbesian region is among the five most species rich regions of the world in terms of avian endemics (61 species), is home to 32 threatened or near threatened birds, and is considered a critical priority for conservation action (Wedge and Long 1995, BirdLife International 2003). I examined if and how mixed species flocks are impacted by habitat changes that commonly occur throughout the Tumbesian region and much of the rural tropics when local communities harvest trees and graze large numbers of livestock. I expected that habitat degradation would alter food and predator abundances, which would then alter the behavior of nuclear flocking species and the costs and benefits of flocking—ultimately leading to changes in flock characteristics such as diversity and numbers of individuals (Bierregaard and Lovejoy 1989, Thiollay 1992, Stratford and Stouffer 1999, Thiollay 1999, Telleria et al. 2001, Maldonado-Coelho and Marini 2004). Specifically, I predicted that in more disturbed vegetation: 1) flock species richness and numbers of individuals would be lower, 2) species' flocking propensities would be lower, and 3) the rate of food intake of individuals in flocks would be lower. Flock species richness and numbers of individuals might be lower in more disturbed vegetation either because flocking species are no longer present in the disturbed vegetation or are not participating in flocks as frequently. Given that flocks are omnipresent in tropical habitats and that participants have been shown to enjoy fitness advantages (Jullien and Clobert 2000), it is critical to determine how human land use might affect flocking behavior. Further, by using theoretical expectations related to flocking behavior, foraging and predator avoidance, I can start to evaluate why flocking behavior might differ across a disturbance gradient and thus gain insight into how best to conserve mixed species associations.

Methods

Study Site

I conducted this research in Machalilla National Park on the south-western coast of Ecuador. The park is one of the largest in the Tumbesian region (55,095 ha), and contains 67% of its endemic birds (Wedge and Long 1995). The park has a marked gradient of rainfall caused by differences in elevation (0 to 860 m) and slope position relative to the coast. As a consequence, the vegetation gradient ranges from arid scrub at the lowest elevations nearest to the ocean to tropical dry forest further inland to humid and fog forest up in the hills, and generally represents the vegetation types found more broadly across the entire Tumbesian region. Despite its status, many areas within the park suffer from continual degradation from human use, and the rest of the vegetation is in some stage of recovery from excessive grazing and removal of trees for charcoal production (Zambrano and Vargas 1998). Several small communities still exist within the park and residents make a living by farming goats, cattle, horses and pigs—all of which roam freely in the park and cause considerable damage to the vegetation (pers. obs).

I studied mixed species flocks in two common vegetation types within the park—arid scrub and tropical dry forest—under two disturbance levels each (low and moderate), for a total of four different vegetation/disturbance combinations. Arid scrub consists primarily of low, bushy trees and cacti and has an average canopy height of 4.84 (±0.25) m. Prominent plant species in arid scrub include *Caesalpinia corimbosa*, *Cordia lutea* and *Armatocereus cartwightianus*. Tropical dry forest is similar to arid scrub, but differs by having trees with diameters more than twice that of the biggest trees in arid scrub, an average canopy height of 8.19 (±0.50) m, and greater canopy density. Trees that are common in tropical dry forest include *Ceiba trichistandra*, *Zizyphus thyrsiflora* and *Mutingia calabura*. Low disturbance sites are in a part of the park that has been protected from most rural community activities for over 30 years. Moderate disturbance sites are next to rural communities where people often harvest trees and shrubs for charcoal production and house building and allow their cattle, goats, horses and pigs to roam freely. To verify these *a priori* disturbance classifications I recorded the abundances of domestic animals each month along the same transects used for bird counts (see below) and evaluated plant species richness in a series of vegetation plots. Field work was conducted during the short rainy seasons from February to May of each year, when both arid and dry forests flush green leaves and the birds of the region breed. Most of the vegetation remains leafless for the rest of the year, although vegetation in tropical dry forest riverbeds retains moisture year-round and thus maintains leaves much longer.

Vegetation Sampling

Vegetation measurements provided information on local habitat characteristics at each site, and were used to quantify differences among vegetation types and disturbance levels. These measurements, based on Martin et al. (1997) and adapted for use in tropical habitats, are made once at a minimum of ten locations along transects at 200 m intervals in each vegetation type. Vegetation plots consisted of two circles, with 11.3 m and 5 m radii. In the 11.3 m radius circle I recorded: 1) number of stems of all trees and shrubs in each diameter at breast height (DBH) size class by species, with size classes (in centimeters) being 3-8, 8-15, 15-23, 23-38, and >38 DBH; and 2) heights of all trees and shrubs by species in each of the following size classes (in meters): 1-2, 2-5, 5-10, 10-20, >20. In each 5 m radius circle I recorded: 1) the height and species of the tallest tree or shrub, median tree height, most common tree or shrub and how many; 2) an ocular estimate of canopy cover and species providing the most cover; 3) aspect, inclination and elevation and leaf litter depth; 4) an ocular estimate of percent of the ground covered by the following: weeds, grass, shrub, dead sticks, cactus, leaves, water, dead trees and bare soil; 5) number of stems of all trees and shrubs taller than 10 cm in each DBH size class by species, in the same size classes as above with the addition of a <3 cm size class; and 6) heights of all trees and shrubs by species in the same size classes as above with the addition of a 0.5-1 m class. In all plots shrub and trees larger than 10 cm tall were identified to species level according to Foster et al. (1992) and Hernández and Josse (1997).

Community and mixed species flock sampling

Evaluating how vegetation type and degradation level influenced flocking characteristics in this system required obtaining four types of data: 1) the abundance of flocking species with respect to the entire community, 2) species composition and abundances in mixed flocks, 3) the flocking propensity of species in the community, and 4) the foraging rates of species in flocks. I defined a mixed flock as more than one species traveling at a maximum of 10 m from any other species in the flock for at least 10 minutes (birds in pairs or family groups were counted as solitary; Moynihan 1962, Hutto 1994). The first data type provides an evaluation of overall community changes. The second and third data types provide a comparison with the first to assess the extent to which differences in flock composition in a vegetation type/disturbance level result from differences in species' abundances versus their flocking propensities. The fourth data type allows for determining whether birds in flocks were obtaining food at the same rate in the different vegetation types/disturbance levels. Obtaining these data required four different sampling protocols (census walks) in each vegetation type/disturbance level from Feb to May of 2008 and 2009, detailed below. Henceforth, I will refer to each data type with its corresponding number above (1-4).

Data type 1: To compare species richness and relative abundances of all birds in each vegetation/disturbance combination, I completed one 1.8 km line transect count in each combination each month. Transect counts had a fixed detection distance of 50 m. In this method, the observer walks at a constant rate (e.g., 500 m/hr) along a pre-determined route and notes all birds seen or heard within the distance band (Bibby et al. 1992). I began all censuses at approximately 06:40 and ended before 10:30. Since I did not count birds in more than one detection belt I did not estimate species' relative densities or detection probabilities.

Data type 2: I recorded the composition of mixed flocks by systematically walking through each vegetation type/disturbance level. I was careful to uniformly cover each site so that the same mixed flocks are not encountered repeatedly. I followed mixed flocks for between 10 to 30 minutes to ensure that I recorded all individuals present in each flock, while minimizing the possibility that some individuals dropped out of the flock as it passed beyond the home range of an individual bird (Latta and Wunderle 1996). Flocks remained active throughout the day, with no apparent resting period. For each flock encountered I recorded all species and numbers of individual birds present.

Data type 3: To obtain flocking propensities of as many species as possible, I systematically walked existing paths or transects within each vegetation type from one hour after sunrise to one hour before sunset once a month, so that each vegetation/disturbance combination was covered during one census day. I noted whether each bird observed was in a flock or solitary, and calculated flocking propensities by combining observations from all flocking propensity surveys in a vegetation type and dividing the number of flocking individuals of a species by their total detections in these surveys (Jullien and Thiollay 1998, Pomara et al. 2007).

Data type 4: To determine if species obtained food at the same rate across habitats and disturbance combinations I focused on the following subset of species for which I could gather sufficient data to estimate feeding rates: crimson-breasted finch (*Rhodospingus cruentus*), collared antshrike (*Sakesphorus bernardi*), and necklaced spinetail (*Synallaxis stictothorax*), red-eyed vireo (*Vireo olivaceus*), southern beardless-tyrannulet (*Camptostoma obsoletum*), tropical gnatcatcher (*Polioptila plumbea*), and tawny-crowned pygmy-tyrant (*Euscarthmus meloryphus*). All birds are in flocks during these observations except for the crimson-breasted finches, which are all observed out of flocks. I determined species' foraging rates by recording the time in seconds between two food captures for individuals where it was possible to see four consecutive captures. I did this for 30 individuals of each focal species in each vegetation type, for a total of 90 time intervals per species per vegetation type.

Finally, while collecting data types 1-3 I also identified nuclear species. Designation as a nuclear species was based on: large intraspecific group sizes, high flocking propensities, regularity of occurrence in flocks, conspicuous calls or behavior, and leadership role in the flocks (Moynihan 1962, Hutto 1994, Goodale and Beauchamp 2010).

Statistical analyses

Before performing analyses all variables were tested for normality and homogeneity of variances. If parametric assumptions were not met, even after transformations of the data, I used non-parametric tests. To compare the average numbers of domestic animals and mean species richness of trees and shrubs in each vegetation type I used a Kruskal-Wallis test with Mann-Whitney U tests for non-parametric pairwise comparisons. To test for differences among the vegetation types in terms of densities of stems, plant heights and percentages of different types of cover I used a non-parametric multi-response permutation procedure (MRPP; Mielke and Berry 2001), which is a multivariate technique based on an analysis of a rank-transformed distance matrix (McCune and Grace 2002).

Data types 1 and 2: I calculated species richness of the community and mixed flocks for each vegetation type using sample-based rarefaction curves rescaled to the number of individuals, to account for differences in the number of individuals or flocks sampled (Gotelli and Colwell 2001, Lee et al. 2005). To determine whether flocking species were more common in less disturbed vegetation types I also plotted rarefaction curves using only the counts of species that flock at least part of the time, taken from the community transect surveys. Rarefaction curves were calculated using EstimateS (Colwell 1997). To estimate the relative abundance of each species recorded in the transect counts I divided the count of a given species in each vegetation type by the total number of detections for all species in that vegetation type. I then compared the abundances of nuclear flocking species across the vegetation types and disturbance levels using Kruskal-Wallis tests.

Data type 2: To compare the average species richness and number of individuals per mixed flock by vegetation type I first used a Kruskal-Wallis test with Mann-Whitney U tests for pairwise comparisons. I then used a generalized linear model with a Poisson error term and a log-link function (log-linear model) to determine if the average species richness and number of individuals in mixed flocks are influenced by vegetation type, disturbance level, census month or year.

To determine how mixed flock species composition was influenced by vegetation type I used nonmetric multi-dimensional scaling (NMS) to ordinate flocks in species space, using the autopilot “slow and thorough” mode with a random starting configuration, 500 runs, and Sorensen distance as the dissimilarity measure (McCune and Grace, sensu Lee et al. 2005). NMS is an iterative optimization method that attempts to place n samples on k axes so that the rank order of the distances between samples agrees with the rank order of the original distances in the data matrix, with “stress” being a measure of the final lack of agreement in these two sets of ranks (McCune and Grace 2002). I used NMS because it avoids the assumption of linear relationships among the variables, is well suited for data with many zeros, allows for the use of any dissimilarity measure, and positions sample units (flocks) according to covariation and association among the species (indirect gradient analysis; McCune and Grace 2002). I also used a MRPP to provide a non-parametric multivariate test for differences in the flocks and bird communities among the vegetation types (McCune and Grace 2002, Lee et al. 2005).

Data type 3: I used Mann-Whitney U tests to compare the overall flocking propensities of species (listed in Table 3) in each pairwise combination of vegetation types and disturbance levels. To obtain a measure of how widespread or restricted each species was to flocks in a particular vegetation type I ran an indicator species analysis on the flocks following Dúfrene and Legendre (1997) and tested for significance of indicator values with a Monte Carlo technique (McCune and Mefford 1999). This method combines information on each species' abundance and regularity of occurrence in flocks in each vegetation type to provide an indicator value for that species for that vegetation type, and can be used to evaluate the conservation potential of a particular vegetation type (Graham and Blake 2001, Renjifo 2001). To test for differences in feeding rates of species in flocks in different vegetation types and disturbance levels I used a one-way ANOVA and Tukey's HSD post-hoc tests. I ran the MRPPs, NMS and indicator analysis in PC-ORD (McCune and Mefford 1999). All other analyses are run in SPSS (2010).

Results

Vegetation plot differences

The mean species richness of trees and shrubs differed across vegetation types and disturbance levels ($\chi^2 = 53.62$, 3 *df*, $P < 0.001$). Multiple comparisons showed that the mean species richness of trees and shrubs was greater in less disturbed tropical dry forest compared to more disturbed tropical dry forest ($U = 2662$, 1 *df*, $P < 0.001$), and in less disturbed arid scrub compared to more disturbed arid scrub ($U = 5692$, 1 *df*, $P < 0.001$). The MRPP showed that all vegetation types differed significantly in terms of densities of stems, plant heights and percentages of different types of cover (Table 1). The mean number of domestic animals also differed across vegetation types and disturbance levels ($\chi^2 = 61.58$, 3 *df*, $P < 0.001$). Multiple comparisons revealed that more disturbed tropical dry forest had much higher numbers of domestic animals than less disturbed tropical dry forest ($U = 0.000$, 1 *df*, $P < 0.001$), and that more disturbed arid scrub had much higher numbers of domestic animals than less disturbed arid scrub ($U = 0.000$, 1 *df*, $P < 0.001$).

Community and mixed flock censuses

Mixed species flocks of birds occurred in all of the vegetation types in the park, with participants including 25 endemic species, four of which are listed as endangered or vulnerable (IUCN 2010). I observed a total of 99 bird species during transect counts (data type 1, Table 2) and a total of 431 flocks during flock censuses (data type 2, Table 3) in the four vegetation type/disturbance level combinations, with 54 different species participating. I obtained sufficient sample sizes to estimate flocking propensities for 55 species (data type 3, Table 4) and feeding rates for seven species (data type 4, Table 5).

Data type 1: The community transect counts showed that less disturbed tropical dry forest had higher species richness than arid scrub, and less disturbed vegetation had higher species richness than more disturbed vegetation (Table 2). The total number of flocking species and their abundances in the community transect counts showed this same pattern, but did not differ as much across the disturbance gradients as the total numbers of species in the community (Table 2). The numbers of flocking species were slightly lower in more compared to less disturbed vegetation in tropical dry forest (46 species compared to 50).

Data type 2: The mean species richness of flocks differed across the vegetation and disturbance gradients ($\chi^2 = 71.82$, 3 *df*, $p < 0.001$), as did the mean numbers of individuals per flock ($\chi^2 = 79.87$, 3 *df*, $p < 0.001$, Table 3). In both cases, pairwise comparisons revealed that less disturbed tropical dry forest had higher flock species richness and numbers of individuals than more disturbed tropical dry forest and both disturbance levels of arid scrub ($p < 0.001$ for both). However, there were no significant differences in the mean species richness or numbers of individuals in flocks in less disturbed arid scrub compared to more disturbed arid scrub (p = 0.626 and 0.971, Table 3). Generalized linear model results matched the Kruskal-Wallis test results, showing that the flock species richness and numbers of individuals were influenced by vegetation type and disturbance level (Likelihood ratio $\chi^2 = 86.813$, 3 df, $p < 0.001$) but not month (Likelihood ratio $\chi^2 = 1.748$, 3 df, $p = 0.626$) or year (Likelihood ratio $\chi^2 = 0.713$, 1 df, $p = 0.398$).

The MRPP analysis, used to determine the magnitude of differences between flocks across the vegetation and disturbance types, showed that flocks were similar across the disturbance regime in arid scrub vegetation, but in tropical dry forest the flocks are different both from those in arid scrub and across the disturbance regime (Table 6). The NMS, used to compare the species composition of flocks across the vegetation and disturbance types, corroborated these results and gave a final optimum three-dimensional ordination space with a final stress of 19.11, a stress level below 20 is considered to give appropriate confidence to the results of this type of analysis (McCune and Grace 2002). The NMS axes one through three explained 31%, 25%, and 20% of the variance, respectively. Flocks were plotted in species space, and the distance between two flocks in the ordination represents the relative dissimilarity in their species compositions (Fig. 2, sensu Lee et al. 2005). Most species appeared to have strongest affinities for mixed flocks in less disturbed tropical dry forest (represented by radiating lines in Fig. 2), a result that was corroborated with species' flocking propensities and the indicator species analysis.

Comparison of data types 1 and 3: Many of the remaining flocking species in more disturbed tropical dry forest showed much lower propensities to flock than those in less disturbed tropical dry forest; 31 out of 51 species (61%) showed higher flocking propensities or were only present in less disturbed compared to more disturbed tropical dry forest ($U = 481.500$, 1 df, $p = 0.011$, Table 4). In arid scrub, there were more flocking species in less disturbed compared to more disturbed vegetation (32 species compared to 26). However, the flocking propensities of the remaining flocking species did not change much across the disturbance gradient; 11 out of 35 species (31%) showed higher flocking propensities or were only present in less disturbed compared to more disturbed arid scrub ($U = 572.500$, 1 df, $p = 0.946$, Table 4). The total number of species in flocks taken from flock observations (data type 2) also showed that overall, flocks in less disturbed tropical dry forest had the greatest species richness and numbers of individuals, followed by more disturbed tropical dry forest, less disturbed arid scrub and more disturbed arid scrub (Table 3, Fig. 1). The species I identified as nuclear in flocks in both tropical dry forest and arid scrub were the endemic collared antshrike and necklaced spinetail; and the non-endemic red-eyed vireo and tropical gnatcatcher. The abundances of these nuclear species taken from community transect counts did not change much across the vegetation types and disturbance levels (all species had Kruskal-Wallis test p values > 0.001, Table 7).

Many more species had high indicator values for flocks in less disturbed tropical dry forest than in any other vegetation type (Table 8). A majority of these species are not found in arid scrub vegetation but are present across the disturbance gradient in tropical dry forest. Others, such as the bran-colored flycatcher (*Myiophobus fasciatus*) and southern-yellow grosbeak (*Pheucticus chrysogaster*) are common in both tropical dry forest and arid scrub. The three species that had high indicator values for flocks in less disturbed arid scrub are endemic to the Tumbesian region, and two (collared warbling-finch (*Poospiza hispaniolensis*) and Tumbesian tyrannulet (*Phaeomyias tumbezana*)) are found only in arid scrub (Table 8). The Ecuadorian piculet (*Picumnus sclateri*) and streaked saltator (*Saltator striatipectus*) had high indicator values for more disturbed arid scrub, although they are present in all vegetation types.

Data type 4: Feeding rates were higher for all species observed in flocks (and crimson-breasted finch outside of flocks) in less disturbed tropical dry forest compared to more disturbed tropical dry forest, and in less disturbed arid scrub compared to more disturbed arid scrub (Table 5).

Discussion

Habitat degradation due to rural community activities such as tree cutting and livestock grazing is pervasive in tropical environments, yet little knowledge exists regarding if and how native fauna is impacted. Small-scale livestock grazing may have minimal negative impacts and might provide a good example of how people can benefit from land use while at the same time conserving biological diversity. I found that in the Tumbesian region of Ecuador, livestock grazing and other rural community activities had little impact on mixed species flocks of birds, but that there were large negative impacts in tropical dry forest vegetation. These results indicate that small scale grazing may not always be detrimental to native fauna, but that results from one area cannot be safely generalized to different vegetation types even within the same landscape. Further, I found that by examining other indicators in addition to species richness I gained a more complete picture of the impacts of these human disturbances. In this case, studying species interactions allowed a greater negative impact from habitat degradation to be seen than if I had looked at species richness and abundance alone. Species interactions are often ignored in habitat suitability studies, and yet this interspecific exchange of information and resources can have large impacts on whole food web functioning (Hector and Wilby 2009, Trawell et al. 2010).

Mixed species flocks have not been previously described from the Tumbesian region of Ecuador, and little is known about the behavior and ecology of many of the region's endemic birds. Since a majority of birds in this region participated to some degree in mixed flocks during the breeding season, flocking behavior is clearly an important part of the biology of these species, as has been found in other tropical regions (e.g., Latta and Wunderle 1996, Sridhar and Sankar 2008). Mixed flocks are very abundant in both tropical dry forest and arid scrub vegetation, with more than half of the species censused in tropical dry forest and about half of the species censused in arid scrub participating to some degree in the flocks. The range of average species richness of the flocks (7.79-11.27) was similar to that observed for mixed flocks in tropical deciduous forest in Mexico (flocks averaged 7.7 species; Hutto 1994) and Hispaniola (flocks averaged 7.1 species; Latta and Wunderle 1996), and falls within the range of flock species richness reported for other areas in the Neotropics (e.g., Powell 1985). However, the numbers of individuals I observed in the flocks (averaging 29.12-52.31) were much higher than have been previously reported in most areas of the Neotropics, except for a high-altitude montane forest in Ecuador (flocks averaged 21.7 and 44.7 individuals; Poulsen 1996). These large group sizes were due primarily to large numbers of conspecifics within the flocks, such as red-eyed vireos, tropical gnatcatchers, necklaced spinetails and thick-billed euphonias (*Euphonia laniirostris*), and also to juveniles joining the flocks with their parents.

My prediction that flocking would be disrupted in more disturbed vegetation was supported in tropical dry forest. Mixed flocks may show lower species richness and abundance in more disturbed areas as a result of one or more different mechanisms. For example, if bird species richness as a whole decreases in more disturbed vegetation then mixed flocks may also be less species rich in these areas. This might happen if there are fewer microhabitats (and thus fewer available niches) or a lower abundance of prey items in these areas (Orians 1969, Connell 1978, James and Wamer 1982, Lee et al. 2005). Many studies do support the notion that flock species richness represents a simple reflection of the species present in a particular area (e.g., Hutto 1994, Latta and Wunderle 1996, Maldonado-Coelho and Marini 2004). Alternatively, mixed flocks may show lower species richness in more disturbed areas not because bird species richness as a whole is lower, but rather because species are lowering their flocking propensities in these areas. For instance, Sridhar and Sankar (2008) found that the propensity of species to flock in rainforest fragments of varying sizes was influenced by habitat structure as well as differences in bird communities between fragments. They suggest that these changes in species' flocking propensities may be linked to habitat-related changes in the selective advantage of flock participation for each species (Sridhar and Sankar 2008). If the advantages of being in a flock are fewer in more open tropical dry forest this might explain the smaller average flock sizes and lower flocking propensities of species in more disturbed sites. In other tropical forests many species are similarly shown to have stronger associations for mixed species flocks in forest interior than in more disturbed areas (Lee et al. 2005, Pomara et al. 2007, Sridhar and Sankar 2008).

Several different factors might influence the selective advantages of flock participation, including: behavior and abundance of nuclear species, variation in food resources, predation risk, and interactions among these factors. Nuclear species are often sit-and-wait foragers that are thought to provide antipredator benefits to other more active flock members via their superior vigilance (Munn 1985, Powell 1985, Terborgh et al. 1990, Jullien and Clobert 2000), or are groups of conspecifics which also likely provide antipredator benefits (Sridhar et al. 2009). It has been suggested that these more vigilant species may benefit from flock participation by gaining a foraging advantage due to the increased flushing of insects by other flock members or stealing food from other flock members, or may not actually benefit at all (Munn 1985, Jullien and Thiollay 1998, Sridhar et al. 2009). In this study, changes in the behavior or abundance of nuclear species were unlikely to explain changes in flock composition and flocking propensity across the disturbance gradient in either tropical dry forest or arid scrub because nuclear species showed fairly uniform representation and abundance in flocks in all areas. In fact, some of the most common species in the flocks in all vegetation types and disturbance levels were nuclear species. Thus, the nuclear species in this region appear to be less sensitive to habitat disturbance than many of the other flock participants.

My results suggest that mixed flock disruption in disturbed tropical dry forest results from both lower community species richness and lower flocking propensities of birds still present in this area. Interestingly, neither mechanism appeared to be operating in arid scrub, where mixed flocks showed little difference in species composition, richness and abundance across the disturbance gradient. Arid scrub vegetation is much more open than tropical dry forest, and thus may afford easier insect capture and a clearer view of predators. While it is possible to hypothesize why flock species richness, composition, and species' flocking propensities changed across the disturbance gradient in tropical dry forest more than in arid scrub, the mechanisms remain speculative. Future studies should focus on understanding the main drivers of flocking in the region—predation pressure and/or foraging benefits—to determine how these factors influence the response of species and flocks to habitat degradation (Sridhar and Sankar 2008).

The foraging rates of the seven species observed are significantly lower in flocks in more disturbed tropical dry forest and arid scrub compared to less disturbed vegetation. This was true for both nuclear and non-nuclear species. While many species enjoy an enhanced foraging rate while in a mixed flock compared to when they are solitary or in pairs (reviewed in Sridhar et al.

2009), few studies have compared foraging rates of birds in flocks across vegetation disturbance levels. While I did not quantify food resources or predators directly, foraging observations should provide a first approximation of whether resource abundance or predators could be influencing flock participation. Birds may enjoy greater foraging efficiencies in less disturbed vegetation due to a decreased need for predator vigilance because of larger flock sizes; or due to increased prey availability via the beater effect, stealing food or learned techniques from other flock members; or greater prey abundance (Sullivan 1984, Powell 1985, Hino 1998). While flock sizes are smaller in more disturbed tropical dry forest than in less disturbed areas, flock size did not change much across the disturbance gradient in arid scrub, and feeding rates are nonetheless lower in the more disturbed vegetation. Thus, lower feeding rates in more disturbed areas of arid scrub, at least, may simply result from lower prey availability. However, truly separating the influence of perceived predation risk and food availability on species' foraging rates was not possible in this study.

Conservation recommendations and future directions

This paper provides a first description of mixed species flocks from Ecuadorian tropical dry forest and arid scrub vegetation. By quantifying flocking behavior in these two vegetation types across a disturbance gradient in Machalilla National Park these results provide new insight into how small-scale clearing of trees and livestock grazing by rural communities influences flocking behavior. Further, the vegetation types found in Machalilla National Park generally represent those that are found more broadly across the entire Tumbesian region, making the results of this study more widely applicable. However, Machalilla National Park is one of the largest protected areas in the region—meaning that most of the remaining Tumbesian region vegetation is under much greater threat of severe degradation.

I have shown that existing park management, which allows community development and livestock grazing within park borders, leads to degradation of the vegetation and disrupts species interactions in tropical dry forest. Moreover, the Tumbesian region is predicted to become drier and more seasonal with climate change (BirdLife International 2003, Miles et al. 2006), and arid scrub vegetation, which requires less rainfall, is likely to replace many areas of tropical dry forest. I found that mixed flocks are more vulnerable to habitat degradation in tropical dry forest than in arid scrub, and thus tropical dry forest and the species found within it should be considered priorities for conservation action. Specifically, my conservation recommendations are to: 1) increase restrictions on livestock grazing and the numbers of houses allowed in existing protected areas in Ecuador and Peru that contain tropical dry forest, 2) designate new protected areas to encompass tropical dry forest that is currently not protected, 3) use predictive models to estimate how tropical dry forest will move with climate change to increase protection of those areas as well, and 4) increase local community awareness of the sensitivity of tropical dry forest to degradation and offer alternative methods of income generation, such as honey production or ecotourism. Other studies of mixed flocks have found that characteristics of mixed species flocks (e.g., diversity) might prove useful as ecological indicators of forest disturbance (Maldonado-Coelho and Marini 2000, 2004, Lee et al. 2005), and the maintenance of flocking behavior is likely crucial for many species' long term persistence. Thus, future management plans for the Tumbesian region should adopt specific strategies such as the ones given here to protect these unique interspecific associations. Further, as this study highlights, interactions between species may be more important to species' persistence than is generally recognized, and researchers should make an effort to learn more about these interspecific associations across taxa and regions.

Ecological and evolutionary theory is increasingly used to evaluate how human-induced habitat alteration will influence biological diversity, and the study of mixed species groups promises to shed light on many areas in community ecology and evolutionary biology (reviewed in Goodale et al. 2010). Mixed species flocks are easily observed and are widespread throughout the world, making them ideal for study. For instance, studies of flock composition and behavior from the range of habitats and geographic areas in which they are found will lead to a better understanding of the evolutionary significance of these unique interspecific interactions (Latta and Wunderle 1996, Sridhar et al. 2009). By using a theoretical framework to evaluate species interactions across a disturbance gradient we can move from simply describing how species abundances change with habitat alteration to understanding why these changes do or do not occur.

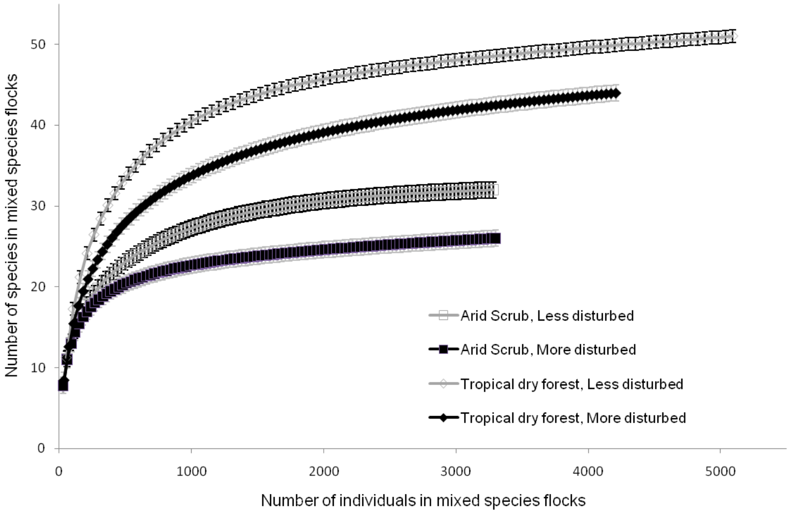

Figure 1. Sample-based rarefaction curves (±SE) of mixed flock species (data type 2) among the vegetation types (arid scrub and tropical dry forest) and disturbance levels (less and more disturbed). Curves are rescaled to the number of individuals.

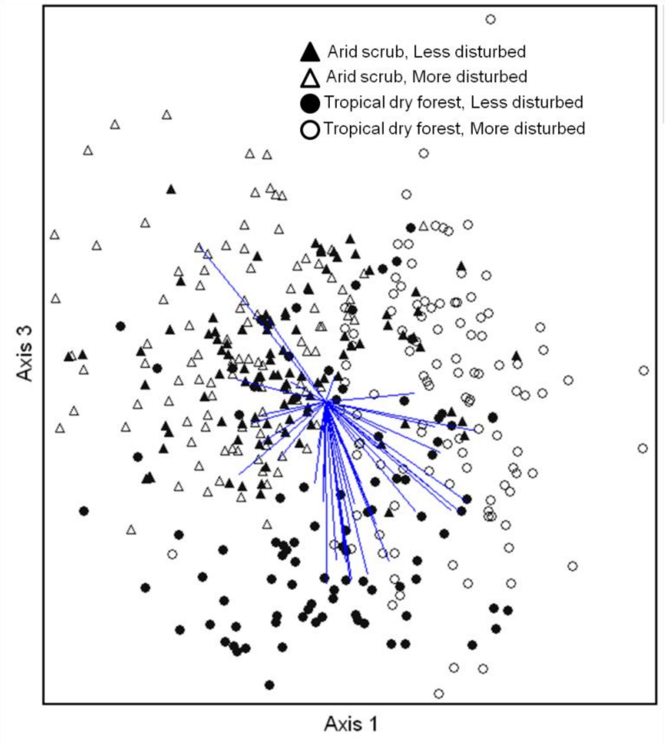

Figure 2. Nonmetric multi-dimensional scaling ordination plot based on the composition and abundance of bird species in flocks in each vegetation type (arid scrub and tropical dry forest) and disturbance level (less and more disturbed; data type 2) (n = 431 flocks). Smaller distances between points represent flocks with more similar species compositions and abundances. Lines represent different species.

Table 1. Multi-response permutation procedure results for vegetation type (arid scrub and tropical dry forest) and disturbance level (LD = less disturbed, MD = more disturbed). Differences based on densities of stems, plant heights and percentages of different types of cover (weeds, grass, shrub, dead sticks, cactus, leaves, water, dead trees and bare soil).

Vegetation types	*T*	*A*	*P*
Arid Scrub LD vs. Tropical dry forest MD	-48.377	0.095	<0.001
Arid Scrub LD vs. MD	-34.806	0.071	<0.001
Arid Scrub MD vs. Tropical dry forest MD	-25.783	-0.047	<0.001
Arid Scrub MD vs. Tropical dry forest LD	-16.508	0.045	<0.001
Arid Scrub LD vs. Tropical dry forest LD	-13.879	0.049	<0.001
Tropical dry forest LD vs. MD	-7.917	0.020	<0.001

T is the test statistic representing the separation between vegetation types (more negative *T*s mean stronger separation; McCune and Grace 2002, Lee et al. 2005). *A* is the chance-corrected within-group agreement describing the within-group homogeneity as compared to random expectation, independent of sample size (McCune and Grace 2002, Lee et al. 2005).

Table 2. Total species richness and numbers of individuals of the community and of only species that participate at least some of the time in flocks, taken from community transect counts (data type 1).

Vegetation type	Total species richness	Total individuals	Total flocking species	Total flocking individuals

Tropical dry forest LD	79	9116	51	7773
Tropical dry forest MD	69	8816	46	7906
Arid scrub LD	57	9660	32	7381
Arid scrub MD	52	8924	26	7780

Table 3. Mean species richness and numbers of individuals per flock, total numbers of species in all flocks, and total numbers of flocks observed in each vegetation type (arid scrub and tropical dry forest) and disturbance level (LD = less disturbed, MD = more disturbed; data type 2).

Vegetation type	Mean species richness(±SE)	Mean individuals (±SE)	Total species	Total individuals	Total flocks observed
Tropical dry forest LD	11.27 (±3.12)	52.31 (±23.32)	51	5091	98
Tropical dry forest MD	8.42 (±3.48)	36.08 (±20.87)	44	4210	115
Arid scrub LD	7.83 (±2.38)	29.12 (±12.42)	32	3280	109
Arid scrub MD	7.79 (±2.74)	29.88 (±14.36)	26	3298	109

Table 4. Flocking propensities for species (n = 55) with more than 20 total observations in a vegetation type (tropical dry forest and arid scrub) or disturbance level (LD = less disturbed, MD = more disturbed; data type 3).

Species	Tropical dry forest LD	Tropical dry forest MD	Arid scrub LD	Arid Scrub MD
Amazilia Hummingbird*	0	0	0	0
Baird's Flycatcher*	0.17	NA	0	0.12
Black and White Becard	0.93	NA	NA	NA
Black-lored Yellowthroat	1	NA	0.31	0.26
Blackish-headed Spinetail*	1	NA	NA	NA
Blue-crowned Motmot	0	0	0	0
Blue-gray Tanager	1	0	NA	NA
Bran-colored Flycatcher	0.92	0.50	0.27	0.36
Collared Antshrike*	0.88	0.80	0.74	0.83
Collared Warbling-Finch*	NA	NA	0.69	0.61
Common Tody-Flycatcher	1	0.63	NA	NA
Crimson-breasted Finch*	0.60	0.14	0.52	0.45
Croaking Ground Dove*	NA	NA	0	0
Ecuadorian Piculet*	1	1	0.73	0.87
Elegant Crescentchest*	1	NA	1	1
Fasciated Wren*	0	0	NA	NA
Golden-olive Woodpecker	0.86	0.61	NA	NA
Gray-capped Cuckoo	1	.53	NA	NA
House Wren	1	1	1	1
Long-tailed Mockingbird*	0	0	0	0
Necklaced Spinetail*	0.89	0.83	0.76	0.74
Olivaceous Woodcreeper	1	NA	NA	NA
One-colored Becard	0.89	1	NA	NA
Pacific Elaenia*	0.62	0.51	0.75	0.83
Pacific Hornero*	NA	0.08	NA	0
Pacific Parrotlet*	0.21	0	0.32	0.22
Pale-browed Tinamou*	0	0	0	0
Parrot-billed Seedeater*	NA	NA	0.67	1
Plain Antvireo	1	0.75	NA	NA
Plumbeous-backed Thrush*	1	0.81	NA	NA

Red-billed Scythebill	0.86	0.69	NA	NA
Red-eyed Vireo	0.75	0.64	0.57	0.51
Red-masked Parakeet*	0	0	0	0
Rufous-browed Peppershrike	1	0.68	NA	NA
Scarlet-backed Woodpecker	1	NA	1	1
Sooty-crowned Flycatcher	1	0.72	0.83	0.91
Southern Yellow-Grosbeak	1	0.74	0.50	0.65
Southern-beardless Tyrannulet	0.84	0.65	0.75	0.75
Speckle-breasted Wren*	1	0.50	NA	NA
Streaked Flycatcher	0	0	NA	NA
Streaked Saltator	0.69	0.43	0.37	0.79
Streak-headed Woodcreeper	1	0.59	1	0.73
Superciliated Wren*	1	0.47	1	0.71
Tawny-crowned Pygmy-Tyrant	0.49	0.48	0.30	0.28
Thick-billed Euphonia	0.53	0.68	NA	NA
Tropical Gnatcatcher	0.92	0.87	0.61	0.55
Tropical Kingbird	0	NA	NA	NA
Tropical Parula	1	NA	NA	NA
Tumbesian Tyrannulet*	NA	NA	0.67	0.49
Vermillion Flycatcher	0	NA	0	0
West Peruvian Dove*	0	0	0	0
White-edged Oriole*	0.64	NA	0.76	0.24
White-tipped Dove	0	0	0	0
Yellow-olive Flatbill	0.50	NA	NA	NA
Yellow-rumped Cacique	0.15	0.18	NA	NA

* are endemic to the Tumbesian region

Table 5. Average foraging rates (time in seconds between two food captures ±SE) for individuals in flocks where it was possible to see four consecutive captures, listed separately for each vegetation type (arid scrub and tropical dry forest) and disturbance level (LD = less disturbed, MD = more disturbed; data type 4). n = 30 individuals of each of the seven species in each vegetation type/disturbance level (three feeding intervals/individual).

Species	Tropical dry forest LD	Tropical dry forest MD	Arid scrub LD	Arid scrub MD	*F*	*P*
Collared Antshrike	39.88* ±0.627	49.78* ±0.827	46.41* ±0.579	50.08* ±0.812	88.076	<0.001
Crimson-breasted Finch	NA	NA	35.02 ±0.575	42.39 ±0.734	62.557	<0.001
Necklaced Spinetail	35.38* ±0.519	43.57* ±0.588	39.07* ±0.445	45.69* ±0.554	75.947	<0.001
Red-eyed Vireo	35.91* ±0.489	43.46* ±0.583	38.43* ±0.508	45.61* ±0.527	71.434	<0.001
Southern Beardless-tyrannulet	38.54* ±0.511	44.43* ±0.549	43.70* ±0.565	51.46* ±0.845	70.772	<0.001
Tropical Gnatcatcher	35.59* ±0.506	43.18* ±0.541	40.78* ±0.560	49.96* ±0.837	91.693	<0.001
Tawny-crowned Pygmy-tyrant	NA	NA	30.11 ±0.312	35.29 ±0.400	104.419	<0.001

* $P < 0.05$ across disturbance gradients in Tukey's HSD pairwise comparisons

Table 6. Multi-response permutation procedure results for mixed flock differences in species composition and abundance among the different vegetation types (arid scrub and tropical dry forest) and disturbance levels (LD = less disturbed, MD = more disturbed; data type 2).

Vegetation types	*T*	*A*	*P*
Tropical dry forest LD vs. Arid scrub MD	-68.440	0.212	<0.001
Tropical dry forest MD vs. Arid scrub MD	-67.667	0.182	<0.001
Tropical dry forest LD vs. Arid scrub LD	-64.284	0.202	<0.001
Tropical dry forest MD vs. Arid scrub LD	-51.896	0.142	<0.001
Tropical dry forest MD vs. LD	-50.592	0.153	<0.001
Arid scrub LD vs. MD	-10.270	0.029	<0.001

T is the test statistic representing the separation between vegetation types (more negative *T*s mean stronger separation; McCune and Grace 2002, Lee et al. 2005). *A* is the chance-corrected within-group agreement describing the within-group homogeneity as compared to random expectation, independent of sample size (McCune and Grace 2002, Lee et al. 2005).

Table 7. Relative abundances of each nuclear flocking species recorded in community transect counts (data type 1) in each vegetation type (arid scrub and tropical dry forest) and disturbance level (LD = less disturbed, MD = more disturbed). Differences in relative abundances across vegetation types are not significant (i.e., $P > 0.001$) for any species based on Kruskal-Wallis .

Nuclear species	Tropical dry forest LD	Tropical dry forest MD	Arid scrub LD	Arid scrub MD
Collared Antshrike	0.027	0.026	0.024	0.022
Necklaced Spinetail	0.100	0.090	0.125	0.115
Red-eyed Vireo	0.111	0.109	0.147	0.130
Tropical Gnatcatcher	0.099	0.092	0.151	0.122

Table 8. Indicator species for flocks in each vegetation type and disturbance level (LD = less disturbed, MD = more disturbed). Indicator values (i.e., Observed and Random) had a $P < 0.05$ based on Monte Carlo tests (5000 permutations). * = endemic to the Tumbesian region.

Species by vegetation type	Observed	Random	1 SD
Arid Scrub LD			
Collared Warbling-finch*	14.5	3.8	1.02
Elegant Crescentchest*	29.3	15.3	1.41
Tumbesian Tyrannulet*	14.8	7.3	1.25
Arid Scrub MD			
Ecuadorian Piculet*	10.3	6.9	1.23
Streaked Saltator	17.7	13.7	1.43
Tropical Dry Forest LD			
Black-capped Sparrow	16.1	2.2	0.81
Blackish-headed Spinetail*	11.3	2.4	0.85
Black and White Becard	19.4	2.4	0.86
Blue-gray Tanager	3.7	1.3	0.65
Bran-colored Flycatcher	7.8	3.9	1.03
Common Tody-flycatcher	4.1	2.1	0.80
Golden-olive Woodpecker*	7.5	2.6	0.90
Gray-capped Cuckoo	4.6	2.3	0.85
Olivaceous Woodcreeper	9.7	1.7	0.74
Plumbeous-backed Thrush*	34.4	4.8	1.10
Red-billed Scythbill	4.9	2.2	0.81
Rufus-winged Tyrannulet	9.7	1.7	0.71
Southern-yellow Grosbeak	16.4	6.9	1.24
Speckle-breasted Wren*	3.7	1.3	0.67
Tropical Parula	9.4	2.2	0.82

Chapter 4 - Rural community activities negatively impact birds' nest survival in the highly threatened Tumbesian region of Ecuador

Introduction

Reduced nesting success is one of the most common causes of long-term population declines of forest birds living in degraded habitat, often due to an increase in nest predation (Chalfoun et al. 2002, Githiru et al. 2005). One widespread activity resulting in habitat degradation for forest birds is livestock grazing (Wassenaar et al. 2007), which in temperate regions has been shown to reduce vegetation cover and to be associated with increased rates of nest predation (Ammon and Stacey 1997, Walsberg 2005, Heltzel and Earnst 2006). However, little is known about the impacts of small-scale livestock grazing (i.e., <100 animals/km^2) and clearing of trees by rural communities on the nest success of tropical forest birds. More generally, evaluating the effects of habitat fragmentation and degradation on nest predation on tropical birds has proved very challenging because of the difficulty of encountering large numbers of nests in tropical regions (Young et al. 2008). Therefore, knowledge regarding the factors influencing birds' nest success in tropical regions continues to lag behind what is known in temperate zones (Young et al. 2008). Here I examine nest survival of 39 bird species across a gradient of grazing intensity in two distinct vegetation types in the Tumbesian region of Ecuador. The Tumbesian region of south-western Ecuador and north-western Peru has high avian endemism (61 species), is home to 32 threatened or near threatened bird species, and is considered a critical priority for conservation action (Wege and Long 1995, BirdLife International 2003). The region has already lost over 95% of its original forest and is now one of the most threatened in the world due to heavy human use, partly in the form of extensive livestock grazing by rural communities (Best and Kessler 1995). Understanding how anthropogenic disturbance affects the nesting success of these species is essential for predicting their long-term persistence in the region.

Numerous factors can influence whether a particular nest is successful or not. For example, variation in rainfall, temperature or other abiotic factors on both short (i.e., daily or weekly) and long (i.e., monthly or yearly) timescales are often tied to fluctuations in both food and predator abundances, leading to variation in nest survival (Dinsmore et al. 2002). Nest placement at both local (e.g., tree species), patch (e.g., amount of vegetation), and landscape (e.g., distance to human development or roads) scales can influence nest survival either negatively or positively due to differences in microclimates, concealment, and predator communities (Young et al. 2008). Nest type (cup vs. cavity or enclosed) has also been shown to affect nest survival; with open cup nests usually showing higher failure rates due to predation (Martin 1995, Knutson et al. 2004). In tropical regions most of these factors have been evaluated using artificial nests, but predators and predation rates have frequently been found to differ between artificial and natural nests (Moore and Robinson 2004, Thompson and Burhans 2004, Robinson et al. 2005).

While abiotic factors and resources can influence nest survival, nest predation is often considered one of the biggest sources of nest failure (Ricklefs 1969, Martin 1988). Birds nesting in tropical regions face an abundance of possible nest predators, perhaps more so than in temperate regions (Skutch 1985, Robinson et al. 2000, Githiru et al. 2005, Young et al. 2008). This may be especially true in fragmented and degraded tropical landscapes, where elevated numbers of nest predators have been documented (e.g., Githiru et al. 2005). This increase in nest predators may be explained by the "meso-predator release" hypothesis, which states that medium-sized predators increase in fragmented and degraded areas due to the decline or disappearance of higher trophic level predators (Turner 1996, Crooks and Soule 1999). In the Tumbesian region, potential nest predators include rats, squirrels (*Sciurus stramineus*) and other small mammals, medium sized mammals such as the tayra (*Eira barbara*) and jaguarundi (*Puma yagouaroundi*), other birds, and snakes. Little is known regarding how the abundances of these potential nest predators change with vegetation degradation.

My primary objective was to test for differences in the daily nest survival of birds in low and moderately disturbed areas of tropical dry forest and arid scrub vegetation in the Tumbesian region of Ecuador. The major form of disturbance is caused by grazing of goats, pigs, cattle and horses. Human alteration of vegetation in the region has been shown to influence several aspects of bird ecology, including flocking behavior and patterns of species composition, especially in tropical dry forest vegetation (Ch. 3). I expected that daily survival rates of nests would also vary across the disturbance gradient, and that nest survival would be greater in less disturbed tropical dry forest and arid scrub vegetation than in more disturbed areas. My secondary objectives were to determine if daily nest survival rates were related to nest type, placement and vegetation covariates. I expected nest survival would be greater for species with enclosed nests than those with open cup nests, and that nest survival would be positively related to the type of plant the nest was placed in (spiny or not), the height of the nest from the ground, the amount of foliage cover immediately surrounding the nest, and the amount of weed and shrub cover within a 5 m radius of the nest. To evaluate how these factors influenced nest survival I used methods which allow the determination of the variation in daily survival rates of nests across habitats while incorporating the effects of biologically meaningful covariates (Dinsmore et al. 2002, Bulluck and Buehler 2008). Finally, using my findings here as well as previous results from the region, I make conservation recommendations to help ensure the long-term persistence of the unique bird communities of the Tumbesian region.

Methods

Study Site

I conducted this research in Machalilla National Park, on the southwestern coast of Ecuador. Machalilla National Park is one of the largest parks in the Tumbesian region (55,095 ha), and contains 67% of its endemic birds (Wege and Long 1995). The park has a marked gradient of rainfall caused by differences in elevation (0 to 860 m) and slope position relative to the coast. As a consequence, the vegetation gradient ranges from arid scrub at the lowest elevations nearest to the ocean to tropical dry forest further inland to humid and fog forest up in the hills, and generally represents the vegetation types found more broadly across the entire Tumbesian region. Despite its status, many areas within the park suffer from continual degradation from human use, and the rest of the vegetation is in some stage of recovery from excessive grazing and removal of trees for charcoal production (Zambrano and Vargas 1998). Several small communities still exist within the park and residents make a living by farming goats, cattle, horses and pigs—all of which roam freely in the park and cause considerable damage to the vegetation (pers. obs).

I examined birds' nest survival in two common vegetation types within the park—arid scrub and tropical dry forest—under two disturbance levels each (low and moderate), for a total of four different vegetation/disturbance combinations. Arid scrub consists primarily of low, bushy trees and cacti and has an average canopy height of 4.84 (±0.25) meters. Prominent plant species in arid scrub include *Caesalpinia corimbosa*, *Cordia lutea* and *Armatocereus cartwightianus*. Tropical dry forest is similar to arid scrub, but differs by having trees with diameters more than twice that of the biggest trees in arid scrub, an average canopy height of 8.19 (±0.50) m, and greater canopy density. Trees that are common in tropical dry forest include *Ceiba trichistandra*, *Zizyphus thyrsiflora* and *Mutingia calabura*. Low disturbance sites were in a part of the park that was set aside for ecotourism and thus has been protected from most rural community activities for over 30 years. Moderate disturbance sites were next to rural communities where people often harvest individual trees and shrubs for charcoal production and house building and allow their cattle, goats, horses and pigs to roam freely. To verify these *a priori* disturbance classifications I recorded the abundances of domestic animals each month along 1.8 km transects within each vegetation type and disturbance level and evaluated plant species richness in a series of vegetation plots within each type, and found that all vegetation types and disturbance levels differed significantly in these attributes (see Ch. 3).

Nest survival

To determine the nest survival of birds in each vegetation type and disturbance level I used Breeding Biology Research and Monitoring Database (BBIRD) methods to search for and monitor nests of all species encountered (Martin et al. 1997). My six assistants and I systematically searched for nests five days a week in 100 ha plots in each vegetation type and disturbance level (each was searched at least twice/week) from mid-January to late May of 2008 and 2009. Both 2008 and 2009 appeared to have similar rainy seasons, although in 2008 there was more rainfall, especially in the hills, causing the riverbeds to fill more frequently and for longer periods. Published rainfall records for these two years from the Instituto Nacional de Meteorología e Hidrología are not yet available. The location of each nest was marked with a GPS and flagging tape (placed at least 5 m from the nest) and nests were visited every two to seven days (more frequently closer to hatching or fledging dates) to check the status of the eggs or chicks or to note cause-specific nest failure. Nests were considered successful if ≥1 chick fledged from the nest for altricial species and if ≥1 egg hatched for precocial species. I also recorded the numbers of chicks that fledged from each nest. Nest contents were viewed using a mirror on a pole, sometimes with the aid of a six meter bamboo ladder. Spinetails, becards, wrens and flycatchers make enclosed nests that are often more than 5 m off the ground, and thus for these species nest status was based on careful observations of parental behavior and nestling noises. Whenever possible a small hole was made in the side of these nests so the contents could be viewed. Parents always quickly repaired the holes and there was no evidence of increased probability of nest failure.

Vegetation sampling

Once use of a nest was completed due to chick(s) fledging or nest failure, detailed nest composition and placement measurements were taken by again following BBIRD methods (Martin et al. 1997). The vegetation in 5.0 m and 11.3 m radius plots centered around each nest were surveyed, allowing a quantitative comparison of vegetation types and placement of each nest within a microhabitat, habitat, and landscape context (Martin et al. 1997). These surveys included the same measurements taken for quantifying general habitat characteristics (Ch. 3) as well as more specific measurements of nest composition, placement, and concealment (Martin et al. 1997). In the 11.3 m radius circle I recorded: 1) number of stems of all trees and shrubs in each diameter at breast height (DBH) size class by species, with size classes (in centimeters) being 3-8, 8-15, 15-23, 23-38, and >38 DBH; and 2) heights of all trees and shrubs by species in each of the following size classes (in meters): 1-2, 2-5, 5-10, 10-20, >20. In each 5 m radius circle I recorded: 1) the height and species of the tallest tree or shrub, median tree height, most common tree or shrub and how many; 2) an ocular estimate of canopy cover and species providing the most cover; 3) aspect, inclination and elevation and leaf litter depth; 4) an ocular estimate of percent of the ground covered by the following: weeds, grass, shrub, dead sticks, cactus, leaves, water, dead trees and bare soil; 5) number of stems of all trees and shrubs taller than 10 cm in each DBH size class by species, in the same size classes as above with the addition of a <3 cm size class; and 6) heights of all trees and shrubs by species in the same size classes as above with the addition of a 0.5-1 m class. In all plots shrub and trees larger than 10 cm tall were identified to species level according to Foster et al. (1992) and Hernández and Josse (1997). Further, in the five meter radius circle centered on each nest I recorded: 1) the species, height, diameter at breast height (DBH), and crown size of the tree the nest was found in; 2) the height of the nest, its orientation on the trunk, distance to the foliage border, distance to the trunk, number of branches supporting the nest and their average diameter, and the percent of cover above the nest and in each cardinal direction; and 3) internal and external measurements of the nest and a description of the nest material. Nest descriptions, including new information for many endemic species, are published in Knowlton (2010).

All field work was conducted from late January to late May of each year, during the rainy season when both arid and dry forests flush green leaves and the birds of the region breed. Most of the vegetation remains leafless for the rest of the year, although vegetation in tropical dry forest riverbeds retains moisture year-round and thus maintains leaves much longer.

Statistical analyses

Because sample sizes were small for most species, I compared nests in each vegetation type and disturbance level by grouping them according to ecological factors likely to be important to nest survival (Young et al. 2008). These groups were as follows: 1) all species together, 2) all cup nests and all enclosed nests separately, and 3) by species for those species with sample sizes of 10 or more nests in more than one vegetation type or disturbance level. Groupings species together and by nest type should be valid because nest predators are unlikely to distinguish nests based on species, but rather are more likely to cue in on nest stage, height and ease of access (Young et al. 2008). From now on, I use the term “daily nest survival (DSR)” to refer to the probability that a nest will survive a single day, and “nest survival” to refer to the probability that a nest will be successful (Dinsmore et al. 2002).

I used the nest survival model in program MARK to model the daily survival of all nests found (White and Burnham 1999, Rotella 2007). This nest survival model is preferable to the traditional Mayfield method (Mayfield 1961, 1975) because it does not assume nests have a constant daily survival rate, allows the mean and variance of the daily survival rate (DSR) to be estimated, allows DSR to be modeled as a function of multiple covariates, and allows for a wide variety of competing models of DSR to be rigorously tested using Akaike’s Information Criterion (AIC_c) model selection, corrected for small sample sizes (Akaike 1973, Dinsmore et al. 2002). I selected a logit link function to incorporate the covariates into the nest survival model. I scaled the dates so that day 1 was the first day of the nesting season, which was the first day a nest was found for each group. I calculated nest survival (the true probability of a nest surviving from initiation to completion) for these groupings in each vegetation type and disturbance level by using 30 days as the total nesting period (laying, incubation and nestling stages) for species with cup nests and 35 days for species with enclosed nests, which were averages for all species based on published records in the region (Marchant 1960, Knowlton 2010).

For each of my three groupings (all species, by nest type, and species specific) I used a hierarchical modeling procedure (Table 1) to model the relationship between DSR and several variables based on a set of *a priori* hypotheses about which factors should contribute to variance in DSR across vegetation types and disturbance levels (below). This type of hierarchical framework is commonly used to avoid testing all possible combinations of the variables of interest, allowing the focus instead to be only on those models deemed *a priori* to make the most biological sense (Bulluck and Buehler 2008, Smith and Wilson 2010). I decided *a priori* to include any model with a value of $\Delta AIC_c < 2$ in the next suite of models (Burnham and Anderson 1998). The first set of models examined the main effects of year and vegetation type/disturbance level on DSR separately and then together, assuming a constant daily nest survival rate (similar to Mayfield's 1961, 1975 method). The second suite of models then fit linear and quadratic time trends, which allow DSR to vary by day of the nesting season, to the best main effect model. The third set of models added the effects of the following covariates on the best model from the previous suite: 1) nest stage when found (constructing, laying, incubating or brooding), 2) nest height, 3) the amount of foliage cover around the nest, 3) whether the nest was in a spiny tree or not, and 4) weed and shrub cover in a 5 m radius plot surrounding the nest. I only included this limited set of covariates because the other nest placement and vegetation characteristics taken in the vegetation plots (above) were correlated with these variables, and these selected covariates were the ones I deemed to be most biologically relevant in this study system.

I did not test for interactions among covariates or main effects since sample sizes were small and I wanted to retain as much statistical power as possible (Sperry et al. 2008). I determined the degree of support of each model by its Akaike weight (w_i). If the weight of the most supported model was <0.90 I used model averaging to determine the beta coefficients of the covariates in the model and their associated 95% confidence intervals based on unconditional standard errors (Burnham and Anderson 1998). I computed the model averaged parameter estimates using the Akaike weights for each candidate model where the parameter of interest occurred, and only included models with a $\Delta AIC_c \leq 4$ in the confidence set (Burnham and Anderson 1998, Mattsson and Cooper 2009). However, I did not use model averaging for sets of models that included both linear and quadratic time, since the averaged beta estimates may not reflect the hypotheses under consideration (Burnham and Anderson 1998, Blums et al. 2005, Wilson et al. 2007). I interpreted the effect of each covariate of interest on DSR by examining its beta value 95% confidence interval; if the interval included zero then the variable is unlikely to have a strong effect on DSR (Bulluck and Buehler 2008). There is currently no suitable goodness-of-fit test for nest survival models (Dinsmore et al. 2002, Rotella 2007). To compare true nest survival (the proportion of nests that survive from initiation to completion) across the disturbance gradients in arid scrub and tropical dry forest I first calculated models with constant DSR through the breeding season for each of the three groupings. I then raised the given values of DSR to the power of the mean number of days necessary for the species or group of species to finish their nest cycle (laying through brooding; Cooch and White 2007, Borges and Marini 2010).

Lastly, for the five most common species (group 3) I used abundance data taken from linear transect counts through the middle of each nest searching plot (described in Ch. 3) and the total numbers of chicks that successfully fledged of each species to calculate a rough estimate of productivity or "fecundity" in each vegetation type and disturbance level. I pooled all individuals of each species counted in each vegetation type and disturbance level across the four months of the 2008 and 2009 field seasons, and then divided by four to get a rough estimate of the abundances of individuals in each location. I then divided the total number of successfully fledged chicks for each species in each vegetation type and disturbance level by their abundance in that location. This procedure assumes that I was able to find every nest of each of the five species in each plot, which is probably unrealistic though search effort was constant and intensive each month and year. However, these five species have nests that are easy to find (i.e., are usually low to the ground and not well-hidden). Further, my objective was not to gain precise values of fecundity, but rather compare analogous estimates of productivity of these species across vegetation types and disturbance levels. These values are used for comparison with the main findings from the models. I did not use this procedure for nests grouped across species, since it is unlikely that I found every single nest and productivity varies by species.

A priori hypotheses and predictions:

1) Vegetation type / disturbance level: I hypothesized that both vegetation type (arid scrub or tropical dry forest) and disturbance level (less or more disturbed) would affect predator and food source species richness and abundances as well as nest concealment, and therefore DSR. I predicted that in tropical dry forest, which is more vegetatively complex and retains more moisture, predators and food sources would be more abundant and nests would be more greatly concealed, leading to overall higher DSR in tropical dry forest than arid scrub. I also predicted that more disturbed areas of both vegetation types would have fewer predators but also less food and fewer places to conceal nests, leading to lower overall DSR in more disturbed areas.
2) Year: I hypothesized that yearly variation in rainfall, predator abundances and food sources would affect DSR. I predicted that 2008, which had a stronger rainy season, DSR would be higher than in 2009.
3) Linear and Quadratic time: I hypothesized that DSR would vary over the breeding season, due to factors such as parental activity at the nest, predator activity and abundance and changes in rainfall and vegetation characteristics. I predicted that DSR would decline linearly throughout the season, as predators increase in number and cue into nests in later stages (i.e., with nestlings) which are more obvious due to increased parental activity as they bring food to the nestlings (Skutch 1949, Martin et al. 2000). Alternatively, DSR might vary in a curvilinear way if there is a peak or drop in nest survival during the middle of the nesting season.
4) Nest height: I hypothesized that nest height would affect nest predation rate, and predicted that lower nests would be predated more frequently and show lower DSR. This prediction assumes nests are being predated by ground predators such as rats and squirrels; birds can also be a great source of nest predation and thus higher nests might show lower DSR.
5) Cover around the nest: This covariate was estimated as a standardized combination of the percentage of foliage cover hiding the nest in each cardinal direction and from above and below. For example, a nest could be 90% hidden from the west, 50% hidden from the east, 10% hidden from below, etc. These values were then added and divided by six. I hypothesized that the amount of vegetation concealing a nest would affect predator's abilities to locate it, and thus predicted that nests with greater coverage would show higher DSR.

6) Weed and shrub cover in a 5m radius plot around the nest: The amount of weed and shrub cover within 5 m of a nest could either help to conceal the nest from predators or could provide refuge for predators and thus attract them to the nests' vicinity. I therefore made no *a priori* prediction about whether the amount of weed and shrub cover would increase or decrease DSR.
7) Nest stage when found: I hypothesized that the stage of a nest when found (construction, laying, incubating or brooding) would affect the DSR of the nest. I predicted that nests found at a later stage (i.e., brooding) would have a greater likelihood of surviving than nests found during an early stage (i.e., construction or laying), since more vulnerable nests are likely to be predated early on (Smith and Wilson 2010). Nest stage does not necessarily correlate with day of the nesting season, since the birds (even those of the same species) were initiating their nests throughout the breeding season.

Results

Nest survival

I found and monitored a total of 805 nests of 39 species during the two four month field seasons of 2008 and 2009 (Tables 2, 3). Fifty five percent (440) of these nests were successful, and the rest failed due to predation (Fig. 1). Twenty eight percent (222) of the nests were found in less disturbed arid scrub, 29% (233) in more disturbed arid scrub, 14% (116) in less disturbed tropical dry forest, and 29% (234) in more disturbed tropical dry forest. Fourteen percent of nests were found during the construction stage, 19% during the egg laying stage, 44% during the incubation stage, 12% during the nestling stage, and the rest were found during an undetermined stage (enclosed nests only). Due to time and field assistant constraints covariate information was only collected for 633 nests, and thus only these were used in the analyses that include the covariates. This set was not biased because it included a random sample of equal numbers of nests from each species found. The full set of nests was used to determine differences in nest survival of each of the three groupings across the vegetation types and disturbance levels.

Grouping 1: all nests together

The estimates of nest survival generated in each vegetation type and disturbance level from the DSR in the constant survival model showed that nests in more disturbed areas were roughly 1/3 less likely to survive as nests in less disturbed areas of arid scrub and tropical dry forest (Table 4). In the hierarchical procedure the first suite of models indicated that both year and vegetation type/disturbance level had an effect on DSR, and so this model was carried over into the second suite of models. The second suite of models tested the effects of linear time vs. quadratic time on DSR, and showed that linear time was more important than constant or quadratic time on both DSR for all nests. I then included the model with vegetation type/disturbance level, year and linear time in the third suite of models, which indicated that the model including vegetation type/disturbance level, year, linear time, and nest type (cup vs. enclosed), had by far the most support out of the set of models ($w_i = 0.9987$, Table 5). The parameter beta estimates suggested that DSR decreased as the nesting season progressed, were positively affected by less disturbed tropical dry forest and in 2008, and that open cup nests were negatively affected (Table 6). The estimates of DSR as the nesting season progressed showed that daily nest survival decreased slowly as the season progressed in all vegetation types and disturbance levels and was consistently higher by a small amount in less disturbed than more disturbed vegetation in both arid scrub and tropical dry forest (Fig. 2).

Comparison 2: by nest type

I found a total of 612 open cup nests, 184 enclosed nests, and 10 ground nests (Tables 2, 3). The model with the by far the most support for open cup nests with covariate information included a linear time trend, vegetation type/disturbance level, year, and whether the nest was in a spiny plant or not ($w_i = 0.9881$, Table 7). The beta estimates suggested that DSR decreased across the nesting season, was greater in 2008, was positively influenced if nests were in spiny plants, and was greater in less disturbed than more disturbed arid scrub (Table 8). Estimates of DSR across the nesting season showed that DSR decreased slowly as the nesting progressed in all vegetation types and disturbance levels (Fig. 3). Nests in arid scrub showed almost no difference in DSR across the disturbance gradient, while nests in tropical dry forest showed much greater DSR in less disturbed areas than those in more disturbed areas (Fig. 3); nest survival showed the same pattern (Table 4).

The model with the most support for enclosed nests with covariate information included a linear time trend, year and nest stage ($w_i = 0.44$, Table 9). Other models with $\Delta AIC \leq 4$ included height, whether the nest plant was spiny or not, and quadratic time; these models were used for model averaged beta estimates (Table 9). The beta estimates suggested that DSR was negatively affected as the nesting season progressed and for nests found at earlier stages (Table 10). Estimates of DSR across the nesting season showed a slight decrease in DSR as the season progressed, and that even though vegetation type did not show up in the AIC_c models, DSR and nest survival were consistently much higher in less disturbed compared to more disturbed arid scrub, and were slightly higher in less disturbed compared to more disturbed tropical dry forest (Fig. 4, Table 4).

Comparison 3: by species with large sample sizes

During the two years of this study I found a total of more than 10 nests in more than one vegetation type / disturbance level for five species: the crimson-breasted finch (*Rhodospingus cruentus*), necklaced spinetail (*Synallaxis stictothorax*), southern yellow-grosbeak (*Pheucticus chrysogaster*), croaking ground-dove (*Columbina cruziana*) and white-tipped dove (*Leptotila verreauxi*; Table 3). All but the necklaced spinetail make open cup nests (see Knowlton 2010 for more details on the nesting biology of these and other species in the region). These four common open cup nesters made up 63% of the open cup nests I found across the two years of the study, while necklaced spinetail nests made up 55% of total enclosed nests found (Table 3). I only included nest location (i.e., height, cover, weeds/shrubs, whether the plant was spiny or not) covariates for southern yellow-grosbeak nests, since for the other species it would have made the sample sizes too small.

The model that was by far the most supported for White-tipped dove nest DSR included linear time, vegetation type, year and stage ($w_i = 0.9099$, Table 11). The beta values indicated that less disturbed tropical dry forest had a positive impact on DSR, while all nest stages except brooding had a negative effect (Table 12). White-tipped dove nests showed consistently higher DSR and nest survival in less disturbed compared to more disturbed tropical dry forest, and DSR decreased slowly as the nesting season progressed in both disturbance levels (Fig. 5, Table 4).

The DSR model most supported by the data for crimson-breasted finch nests included linear time, vegetation type and year ($w_i = 0.5942$); though these variables with quadratic time instead of linear had a ΔAIC < 2 (Table 13). Beta estimates for the best model suggested that DSR was negatively affected by linear time; but no other estimate was significant (Table 14). DSR for crimson-breasted finch nests consistently decreased as the nesting season progressed with a steep drop around day 45 (Fig. 6). DSR and nest survival were consistently slightly higher in less disturbed than more disturbed arid scrub and tropical dry forest vegetation; though the difference was greater in tropical dry forest (Fig. 6, Table 4).

For necklaced spinetail nests, the DSR model with the most support included only linear time and year, with stage of nest when found added and quadratic time instead of linear also well-supported (ΔAIC < 1, Table 15). Beta estimates for the best model indicated that as the nesting season progressed DSR was negatively affected, and that DSR was higher in 2008 than 2009 (Table 16). Daily survival rates for necklaced spinetail nests decreased slowly across the nesting season and, although vegetation type did not show up in the top AIC_c model, were consistently higher in tropical dry forest than in arid scrub vegetation and in less disturbed compared to more disturbed tropical dry forest (Fig. 7). However, necklaced spinetail DSR was consistently lower in less disturbed compared to more disturbed arid scrub vegetation (Fig. 7). Nest survival for necklaced spinetails showed these same patterns (Table 4).

The DSR model by far best supported for croaking ground-dove nests included quadratic time, vegetation type and stage at which the nests were found ($w_i = 0.9759$, Table 17). However, none of the beta estimates for the top model had 95% confidence intervals that did not cross zero (Table 18). Croaking ground-dove DSR and nest survival were consistently slightly higher in more disturbed compared to less disturbed arid scrub vegetation, and DSR decreased slowly as the nesting season progressed (Fig. 8, Table 4).

The most well supported model by far for southern yellow-grosbeak nests included a linear time trend, vegetation type, year, stage at which the nest was found, nest height, and cover around the nest ($w_i = 0.9315$, Table 19). Beta estimates from this model suggested that linear time had a negative effect on DSR, both less and more disturbed arid scrub had positive effects on DSR, the amount of cover around a nest negatively influenced DSR, and the height of a nest positively influenced DSR (Table 20). DSR and nest survival estimates for the southern yellow-grosbeak were consistently higher in less disturbed arid scrub and tropical dry forest than more disturbed areas, and this difference was much greater between disturbance types in tropical dry forest (Fig. 9, Table 4). DSR declined moderately as the nesting season progressed in all vegetation types and disturbance level except more disturbed tropical dry forest, where there was a steep decline (Fig. 9).

The estimates of productivity for each of the five species in group 3 matched the results for DSR in each vegetation type and disturbance level (Table 22). For example, croaking ground-doves showed higher productivity in more compared to less disturbed arid scrub, which was corroborated with graph of DSR over the nesting season (Fig. 8). Further, necklaced spinetail productivity was greater in more disturbed compared to less disturbed arid scrub, as was also shown in the graph of DSR over the nesting season (Fig. 7). Crimson-breasted finches and necklaced spinetails fledged the most chicks out of the five species (Table 21).

Discussion

Habitat degradation due to rural community activities such as tree cutting and livestock grazing is pervasive in tropical environments, yet little knowledge exists regarding if and how native fauna is impacted (Ch. 3). Small-scale livestock grazing may have minimal negative impacts and has the potential to provide an example of how people can benefit from land use while at the same time conserving biological diversity. However, this study shows that in the Tumbesian region of Ecuador, livestock grazing and other rural community activities do have a negative impact on birds' nest survival for many species, especially in tropical dry forest vegetation. The nest survival of most species examined appeared to be much more greatly negatively impacted by habitat disturbance in tropical dry forest than in arid scrub vegetation. This finding is consistent with previous work in this region, which showed that mixed species foraging flocks of birds are much more negatively impacted by habitat disturbance in tropical dry forest than in arid scrub vegetation (Ch. 3). These results indicate that small scale grazing may not always be detrimental to native fauna, but that results from one area cannot be safely generalized to different vegetation types even within the same landscape. Previous work demonstrated that the abundances of many species in the bird community of Machalilla National Park do not change greatly across the disturbance gradients in arid scrub and tropical dry forest vegetation (Ch. 3). Further, this study suggests many species may be nesting in more disturbed areas of arid scrub and tropical dry forest vegetation as much or even more than in less disturbed areas, despite showing much lower daily nest survival in these areas. Thus, examination of birds' nest survival across this disturbance gradient allowed for a more complete picture of the impacts of human disturbance on the long-term persistence of these species than by examination of species' occurrence and abundance data alone.

Predation, not abandonment or starvation, was the only cause of nest failure in all vegetation types/disturbance levels and years. This result is not surprising given that predation has been cited as the most important cause of nest failure in tropical areas (Martin 1988, Stutchbury and Morton 2001, Borges and Marini 2010). In roughly half of the cases where nests failed there were no remains of the eggs or chicks in or around the nest, suggesting predation from snakes or mammals. Although I was unable to watch nests for predation events using video cameras, I did observe a few predators haphazardly. Rats jumped out of several necklaced spinetail nests as I approached, and the eggs or chicks had been predated. I also observed a rat at the nest of a white-tipped dove and a Guayaquil squirrel methodically eating the chicks in a southern yellow-grosbeak nest. Abundances of rats, squirrels and other nest predators such as some bird species have been shown to increase around human settlements due to waste production (Miller et al. 1998, Borges and Marini 2010), which likely contributes to the lower observed nest survival in these areas compared to more pristine habitat (Robinson et al. 1995, Hobson and Bayne 2000, Phillips et al. 2005, Borges and Marini 2010). Domestic animals in high densities (and their associated feed) may also increase nest predators' densities (Fuller and Gough 1999, Borges and Marini 2010). Nests' DSR always decreased linearly or curvilinearly over the course of the breeding season, due either to predators improving their search image for nests, finding nests more easily due to increased parental activity at nests or increased vocal activity of begging by older chicks in brooding stages, or because of a numerical response by the predators, which should obtain more food and also breed during the rainy season (Nams 1997, Grant et al. 2005).

Grouping 1: all nests together

When nests from all species found were grouped together in each vegetation type and disturbance level, DSR and nest survival were consistently lower in more disturbed areas of both tropical dry forest and arid scrub. Several other studies have reported lower nest survival of birds in more disturbed compared to less disturbed landscapes (Robinson et al. 1995, Hobson and Bayne 2000, Phillips et al. 2005, Borges and Marini 2010). Again, these results are likely due to increases in nest predators in more disturbed habitats, since predation is usually the main cause of nest failure (Ricklefs 1969, Martin 1993). In Machalilla National Park there are high numbers of both rats and squirrels around human settlements; both of which are efficient nest predators and have been shown to increase following human disturbance (Pangau-Adam et al. 2006, Smith and Wachob 2006, Tewksbury et al. 2006). Further, the presence of high densities of domestic animals in more disturbed vegetation likely reduces vegetation cover and thus birds' ability to adequately hide their nests (Fuller and Gough 1999, Borges and Marini 2010). However, I found that cover immediately around a nest and within a 5 m radius was not as important to nest survival as the patch scale variable vegetation type. Further, while I found roughly equal numbers of nests across the disturbance gradient in arid scrub, I found twice as many nests in more disturbed than less disturbed tropical dry forest. This suggests that either these species are preferentially nesting in more disturbed tropical dry forest or that nests are harder to find in this area. Both of these factors were likely important. I found nests of ten species in more disturbed but not less disturbed tropical dry forest; and these species were either disturbance specialists or species that normally prefer more arid vegetation. While these species seemed to be preferentially choosing to nest in more disturbed tropical dry forest, they suffered much lower nest survival than species nesting in less disturbed tropical dry forest. Interestingly, however, the nest survival in more disturbed tropical dry forest was nearly equal to that in less disturbed arid scrub and was much greater than that in more disturbed arid scrub. Thus, more disturbed tropical dry forest may provide a viable alternative nesting location for species that would normally nest in more arid vegetation. Alternatively, differences in predation rates could simply be due to differences in species' specific parental behavior at the nest, and thus grouping multiple species' nests together for analysis may not be valid (Fontaine et al. 2007).

When factors possibly explaining the observed variance in nest survival were examined, linear time, vegetation type, year, and nest type were found to be important. The fact that the broad-scale covariate vegetation type showed up in the model with the most support while none of the local-scale covariates did, such as nest cover or weed and shrub abundance, suggests that overall vegetation complexity may be more important for nest survival than local scale coverage or placement; a result which has been found elsewhere (Filliater et al. 1994, Wilson and Cooper 1998, Huhta et al. 1999, Burhans et al. 2002, Chase 2002, Davis 2005, Bulluck and Buehler 2008). Nest type had a strong influence on DSR, with open cup nests showing lower survival than enclosed nests. This is a common finding and likely results from predators being less able to see and/or enter enclosed nests (Lack 1948, Nice 1957, Martin 1995). In Machalilla National Park enclosed nests were primarily either hung from the outermost branches of large trees where small mammal weight would not be supported, placed adjacent to active wasp nests, or tightly woven from thorny sticks; making it easy to imagine why predators might have a harder time accessing these nests. Further, fasciated wrens (*Campylorhynchus fasciatus*) make large communal enclosed nests, and are probably very successful at group defense of the nest from predators. However, again it is worth emphasizing that parental care behaviors are sometimes observed to be more important than nest type on nest predation rates (Fontaine et al. 2007), and I could not rule out those differences here.

Grouping 2: by nest type

When nests were grouped by species that make open cup and enclosed nests separately, DSR and nest survival were greater in less disturbed than more disturbed tropical dry forest, but surprisingly did not differ much across the disturbance gradient in arid scrub for open cup nests.

Numbers of open cup nests found were equal across the disturbance gradient in arid scrub, but were nearly twice that of open cup nests found in tropical dry forest. Crimson-breasted finch nests made up roughly half the total open cup nest found in both less and more disturbed arid scrub, and nests of the other three common open nesters made up another fourth. Croaking ground-doves had much greater nest survival in more disturbed compared to less disturbed arid scrub, which may contribute to the pattern of little difference in DSR across the arid scrub disturbance gradient seen for all open cup nests in arid scrub. However, it is possible that predation pressure and vegetation complexity differ less substantially across the disturbance gradient in arid scrub than in tropical dry forest. Alternatively, disturbance specialists, such as croaking ground-doves, may fare better in more open areas. Given that open cup nests make up the great majority of all nests found in arid scrub vegetation, the few enclosed nests monitored must be responsible for the greater nest survival observed for all nests in less disturbed compared to more disturbed arid scrub. This is, in fact, what we observe—enclosed nests had more than twice the probability of survival in less compared to more disturbed arid scrub. The reasons for this difference remain speculative; in the future cameras should be set up on enclosed nests in both less and more disturbed arid scrub to determine if predation attempts and predator species differ across this disturbance gradient. Further, sample sizes of enclosed nests were quite small in all areas, with necklaced spinetails making the majority of nests found, except in more disturbed tropical dry forest where the sample sizes of enclosed nests were larger. Thus, further study with larger and more even sample sizes and more species represented may yield different results than those obtained here.

Factors important in explaining the variance in nest survival for open cup nests were linear time, vegetation type, and year; as was the case for all nests together. However, whether a nest was placed in a spiny plant or not also came out as being important. This supports the idea that open cup nests are more vulnerable to predation than enclosed nests, and thus can improve their probability of survival if placed in a naturally protected area such as the middle of a spiny plant. Many plants in the Tumbesian region are very spiny, and it is possible that the birds of the region evolved to exploit this feature when nesting. For enclosed nests, only linear time and nest stage when found were important in explaining the variance in nest survival. Given the longer time period required to construct these large enclosed nests I found a greater proportion in the construction phase than I did for open cup nests, which can be built relatively quickly. Nests in earlier stages may be predated early if they are vulnerable (Smith and Wilson 2010), and the fact that nests found during construction fared worse than those found at later stages supports my *a priori* hypothesis that nests in earlier stages would suffer lower nest survival.

Grouping 3: by species

Of the five species for which I had sufficient sample sizes, necklaced spinetails consistently had the highest nest survival across vegetation types and disturbances levels, while crimson-breasted finches consistently had the lowest. Necklaced spinetails make large, conspicuous, enclosed nests of tightly woven small spiny twigs with a long tunnel entrance on one side (Knowlton 2010), and these nests are likely difficult for predators to enter (though rats were found in a few nests). In contrast, crimson-breasted finches make small, fragile cup nests and place them on branches hidden behind clumps of leaves on small trees and shrubs, primarily in arid scrub vegetation. These nests are easy for human observers to find once a search pattern has been developed, and this is likely true for predators as well, especially when the adults must constantly return to the nest with food for the nestlings. Crimson-breasted finch nests fared much better in less disturbed than more disturbed areas of both arid scrub and tropical dry forest, but only year came out as important in explaining the variance in nest survival. Necklaced spinetails also showed greater nest survival in less disturbed compared to more disturbed tropical dry forest, but had greater nest survival in more disturbed compared to less disturbed arid scrub. This result is unexpected given that enclosed nests did not show this pattern, and yet the majority of enclosed nests found were those of necklaced spinetails. The few enclosed nests that belonged to other species must be responsible for the pattern seen for all enclosed nests together—these species were the southern beardless tyrannulet (*Camptostoma obsoletum*), superciliated wren (*Thryothorus superciliaris*), streaked flycatcher (*Myiodynastes maculatus*) and elegant crescentchest (*Melanopareia elegans*). For necklaced spinetails, linear time, year and stage of the nest when found were the factors important in explaining the variance in nest survival; which is not surprising since these factors were also most important for all enclosed nests together.

White-tipped dove nests had more than twice the likelihood of survival in less disturbed compared to more disturbed tropical dry forest. The sample sizes of nests found of this species were too small to say anything conclusive about differences in nest survival in arid scrub vegetation. White-tipped doves are generalist species that are found in open areas as well as woodland (Ridgely and Greenfield 2001), and I did find a greater number of nests of this species in more disturbed tropical dry forest than in less disturbed areas. Yet, though they may be preferentially nesting in more disturbed areas, the observed lower nest survival and productivity in this vegetation type suggests either the presence of an ecological trap or that competition for nesting sites from other large doves, such as west Peruvian doves (*Zenaida meloda*) or pale-vented pigeons (*Columba cayennensis*), in less disturbed areas is driving the white-tipped doves out of this better habitat. Alternatively, I may have overlooked nests of this species more often in less disturbed than more disturbed tropical dry forest. Vegetation type and nest stage when found were the important factors explaining the variance in nest survival for the doves. The smaller croaking ground-dove had greater nest survival in more disturbed compared to less disturbed arid scrub vegetation, and was not found nesting in tropical dry forest. This species is also a generalist and is found in open areas and even nests in villages and towns, sometimes inside houses. Why this species should suffer lower nest predation in more disturbed areas is unclear—again, cameras at nests across the disturbance gradient could shed light on differences in predation. Like white-tipped doves, the factors most important in explaining variance in nest survival for the croaking ground-doves were vegetation type and nest stage when found, although quadratic rather than linear time was also important. I was unable to test for the effects of nest height, nest coverage, weed and shrub cover and whether the nest was in a spiny plant or not for any of the species separately except the southern-yellow grosbeak, since this information was not collected for a large enough sample of the nests. However, for southern yellow-grosbeaks the covariates that were important in explaining nest survival were vegetation type, cover immediately around the nest and nest height. The grosbeaks had much greater nest survival in less disturbed compared to more disturbed arid scrub and tropical dry forest; although productivity was similar across the disturbance gradient in arid scrub.

Conclusions

My *a priori* hypotheses regarding the sources of variation in nest survival were supported in some cases and not supported in others. For most groupings, day of the nesting season (linear time), vegetation type, year and nest type were important factors explaining variation in DSR. In several groupings the stage at which the nest was found was also important, but in only one group each was nest height, cover around the nest, and whether the nest was in a spiny plant or not important. The amount of weed and shrub cover within 5 m of the nest never showed up in the variables important in explaining variation in DSR. These results suggest that in addition to seasonal variation on both short (daily) and long (yearly) time scales, factors at large spatial scales, such as vegetation type, are more important for nest survival than smaller scale location attributes such as weed and shrub cover or nest placement. Many other studies have also found little effect of smaller scale location and placement variables on DSR (see Bulluck and Buehler 2008 for a complete list). Hypotheses to explain this result that have been suggested are that spatial and temporal variation in predator communities may lead to a lack of consistent natural selection pressures on nest placement (Chase 2002), or that nest site selection may be controlled by factors other than predation (Lenington 1980, Huhta et al. 1999). Alternatively, nest placement at local scales may not have much of an impact of nest predation rates if predators primarily find nests using olfactory cues (i.e., mammalian predators) or if they are able to get to all possible nest locations with equal ease. Another factor that I was unable to consider in this study was parental behavior at the nest. Recent work suggests that birds change their behavior while nesting depending on their perception of predation risk; and that this behavior plays a larger role in whether nests are predated than does nest placement at local or landscape scales (e.g., Ghalambor and Martin 2002, Fontaine et al. 2007). Thus, future studies in the region should control for parental behavior to determine if the patterns found here still remain. For example, parents of some bird species visit the nest at more frequent intervals to bring food to chicks, which could draw predators to the nest. Video cameras or observers counting the number of parental visits per hour to the nest could help to control for this behavior.

The effects of habitat disturbance on birds in the Neotropics deserve further attention, as most studies to date have focused only on forest fragmentation in this region (e.g., Stratford and Stouffer 1999, Marini 2001) or agrosystems (Borges and Marini 2010). This study suffered from the common problem associated with multi-species nest survival studies in tropical regions; low sample sizes. Further, to really understand how predator communities and nest predation differs across the landscape gradient would require constant monitoring of all active nests with video cameras, which proved too costly for this study. Despite these limitations, this paper provides a first description of birds' nest survival across a disturbance gradient in tropical dry forest and arid scrub vegetation in the Tumbesian region, yielding new insights into how small-scale clearing of trees and livestock grazing by rural communities will likely impact the long-term persistence of these species. Further, different species showed different responses to habitat degradation in this landscape, suggesting that grouping nests of all species together may not be the best way to examine the effects of degradation on these species. However, the results from this study support earlier work showing that existing park management, which allows community development and livestock grazing within park borders, leads to degradation of the vegetation and negatively impacts the bird community, especially in tropical dry forest vegetation (Ch. 3). The less-to-more disturbed landscape gradient in Machalilla National Park might be functioning as a source-sink system (Pulliam 1988) for some species (Borges and Marini 2010); especially since many species seemed to preferentially nest in more disturbed areas despite showing lower nest survival there. However, further information is required to determine this; such as whether birds in more disturbed areas also experience reduced adult survival, juvenile survival or number of renesting attempts in addition to reduced nest survival (Young et al. 2008). Therefore, additional study of the effects of livestock grazing on the bird community in Machalilla National Park is warranted, to determine if taking measures such as lowering the density of livestock and restricting human activities within the park should be taken to ensure the long term survival of the unique bird communities of the Tumbesian region.

Table 1. The variables associated with each suite of models of daily nest survival and the corresponding notation. Combinations of variables are not shown.

Model Suite	Variables	Notation
1	Single estimate of daily survival	$S_{(.)}$
	Year	$S_{(year)}$
	Vegetation type/ disturbance level	$S_{(veg\ type)}$
2	Linear time	$S_{(T)}$
	Quadratic time	$S_{(TT)}$
3	Nest stage	$S_{(stage)}$
	Nest type	$S_{(nest\ type)}$
	Nest height	$S_{(height)}$
	Nest cover	$S_{(cover)}$
	Plant type (spiny or not)	$S_{(plant)}$
	Weed and shrub cover	$S_{(weeds/shrubs)}$

Table 2. Total number of active nests encountered in 2008 and 2009 combined in each vegetation type (arid scrub and tropical dry forest) and disturbance level (LD = less disturbed, MD = more disturbed) by species. Nest type of each species is also given; C = open cup, G = ground, E = enclosed.

Species	Nest type	Arid scrub LD	Arid scrub MD	Tropical dry forest LD	Tropical dry forest MD
Rufous–necked Woodrail	C	0	2	0	0
West Peruvian Dove*	C	5	2	9	8
Croaking Ground–dove*	C	29	29	0	4
Eared Dove	C	0	0	3	4
White–tipped Dove	C	4	2	20	30
Paraque	G	2	2	2	0
Gray–capped Cuckoo	C	7	5	9	2
Short–tailed Woodstar	C	1	0	0	0
Necklaced Spinetail*	E	14	19	12	57
Collared Antshrike*	C	1	3	5	17
Plain Antvireo	C	0	0	0	3
Elegant Crescentchest*	G/E	2	1	0	0
Common Tody-flycatcher	E	0	0	0	1
Southern Beardless–tyrannulet	E	3	5	3	25
Tumbesian Tyrannulet*	C	1	0	0	0
Yellow–olive Flatbill	E	0	1	0	3
Tawny–crowned Pygmy–tyrant	C	3	9	1	0
Bran–colored Flycatcher	C	0	1	4	0
Vermillion Flycatcher	C	0	13	0	0
Streaked Flycatcher	E	0	1	0	2
Black–and–White Becard	E	0	0	1	3
One–colored Becard	E	0	0	3	16
Fasciated Wren*	E	0	0	0	13
Speckle–breasted Wren	G/E	0	0	1	0
Superciliated Wren	E	0	2	0	1
Long–tailed Mockingbird*	C	9	0	0	7
Tropical Gnatcatcher	C	5	7	4	0
Rufous–browed Peppershrike	C	0	0	1	1
Red–eyed Vireo	C	2	9	4	2

Plumbeous–backed Thrush*	C	0	0	5	0
Streaked Saltator	C	11	0	8	1
Southern Yellow–grosbeak	C	12	15	11	7
Thick-billed Euphonia	C	0	0	0	1
Parrot–billed Seedeater*	C	1	1	0	0
Crimson–breasted Finch*	C	106	95	12	8
Collared Warbling–finch*	C	4	4	0	0
White–edged Oriole*	C	0	0	0	2
Smooth-billed Ani	C	0	2	2	8
Scrub Blackbird	C	0	0	0	4

Figure 1. Total numbers of nests found and the total number that failed (percentage failure shown at the top of each pair of bars) in each vegetation type (arid scrub and tropical dry forest) and disturbance level (LD = less disturbed, MD = more disturbed) in 2008 and 2009 combined.

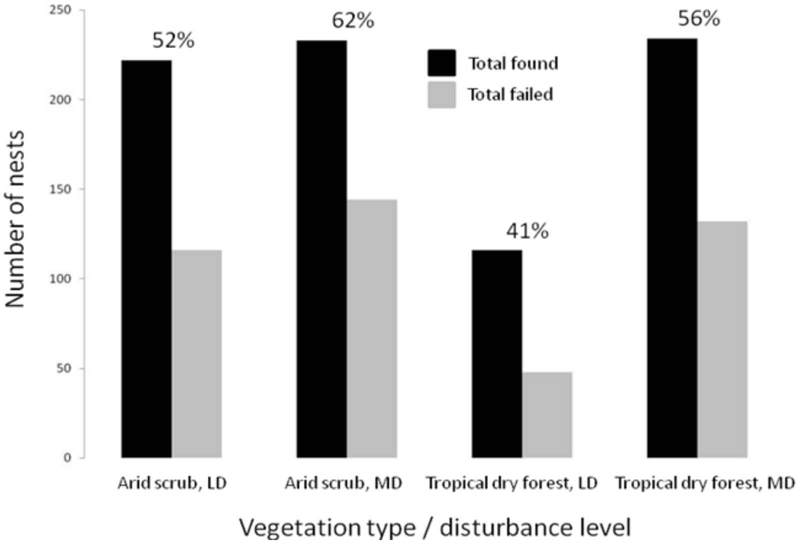

Table 3. Total numbers of nests found, nests with covariate information, open cup nests, enclosed nests, and of each of the five most common species in less disturbed (LD) and more disturbed (MD) arid scrub and tropical dry forest vegetation in 2008 and 2009 combined in Machalilla National Park, Ecuador. Total numbers of species represented are shown in parentheses.

Vegetation type	Total nests	Total with covariates	Total open cup	Open cup with covariates	Total enclosed	CBFI	CGDO	SYGB	WTDO	NEST
Arid scrub, LD	222 (20)	144	201 (16)	125	19 (4)	106	29	12	4	14
Arid scrub, MD	233 (23)	173	201 (16)	144	29 (7)	96	29	15	2	19
Tropical dry forest, LD	116 (21)	108	94 (15)	89	19 (6)	12	0	11	20	12
Tropical dry forest, MD	234 (25)	205	116 (16)	102	118 (9)	8	4	7	30	57

CBFI = crimson-breasted finch, CGDO = croaking ground-dove, SYGB = southern yellow-grosbeak, WTDO = white-tipped dove, NEST = necklaced spinetail

Table 4. Daily survival rates and nest survival (DSR^{30} or DSR^{35} for enclosed and spinetail nests) for all nests together, for open cup and enclosed nests separately, and for each of the five species with the largest sample sizes by vegetation type (arid scrub and tropical dry forest) and disturbance level (LD = less disturbed, MD = more disturbed) in 2008 and 2009 combined.

Vegetation Type	Arid scrub, LD		Arid scrub, MD		Tropical dry forest, LD		Tropical dry forest, LD	
	DSR	True nest success	DSR	True nest success	DSR	True nest success	DSR	True nest success
All nests	0.953	24%	0.938	14%	0.970	40%	0.955	25%
Open cup	0.947	20%	0.950	21%	0.969	39%	0.925	10%
Enclosed	0.971	36%	0.947	15%	0.980	49%	0.970	34%
CBFI	0.922	9%	0.898	4%	0.961	30%	0.927	10%
CGDO	0.930	11%	0.963	32%	N/A	N/A	N/A	N/A
NEST	0.955	20%	0.970	34%	0.986	66%	0.978	51%
SYGB	0.969	39%	0.938	15%	0.985	59%	0.821	0%
WTDO	N/A	N/A	N/A	N/A	0.979	53%	0.950	21%

Table 5. Model selection results for daily nest survival for all nests together in less and more disturbed arid scrub and tropical dry forest vegetation in Machalilla National Park, Ecuador in 2008 and 2009.

Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Parameters	Deviance
$S_{(\text{T+veg type+year+nest type})}$	2939.423	0	0.9987	1	7	2925.415
$S_{(\text{T+veg type+year+stage})}$	2952.65	13.227	0.0013	0.0013	9	2934.637
$S_{(\text{T+veg type+year+plant})}$	2966.624	27.2003	0	0	7	2952.615
$S_{(\text{T+veg type+year+height})}$	2970.413	30.9895	0	0	7	2956.404
$S_{(\text{T+veg type+year})}$	2984.771	45.3475	0	0	6	2972.765
$S_{(\text{TT+veg type+year})}$	2984.821	45.3972	0	0	7	2970.812
$S_{(\text{T+veg type+year+cover})}$	2984.911	45.4872	0	0	7	2970.902
$S_{(\text{T+veg type+year+weeds/shrubs})}$	2986.391	46.9672	0	0	7	2972.382
$S_{(\text{veg type+year})}$	3053.892	114.4686	0	0	5	3043.887
$S_{(\text{year})}$	3065.347	125.9232	0	0	2	3061.346
$S_{(\text{veg type})}$	3068.666	129.2424	0	0	4	3060.663
$S_{(.)}$	3080.551	141.1277	0	0	1	3078.551

Table 6. Beta estimates and 95% confidence intervals for parameters in best model for all nests in less and more disturbed arid scrub and tropical dry forest vegetation in Machalilla National Park, Ecuador in 2008 and 2009.

Parameter	β Estimate	SE	Lower 95% CI	Upper 95% CI
b0	47.9336	1.9075	44.1948	51.6724
Linear time*	-0.2759	0.0357	-0.3457	-0.2060
Arid scrub, LD	0.1524	0.1426	-0.1272	0.4320
Arid scrub, MD	0.1727	0.1354	-0.0926	0.4381
Tropical dry forest, LD*	0.6968	0.1759	0.3520	1.0417
Year*	0.2291	0.1120	0.0096	0.4486
Nest type*	-0.8624	0.1310	-1.1192	-0.6057

* means the covariate is significant (i.e., confidence interval does not include zero)

Figure 2. Daily nest survival rate of all nests together as the nesting season progressed in less disturbed (LD) and more disturbed (MD) arid scrub and tropical dry forest in 2008 and 2009 combined.

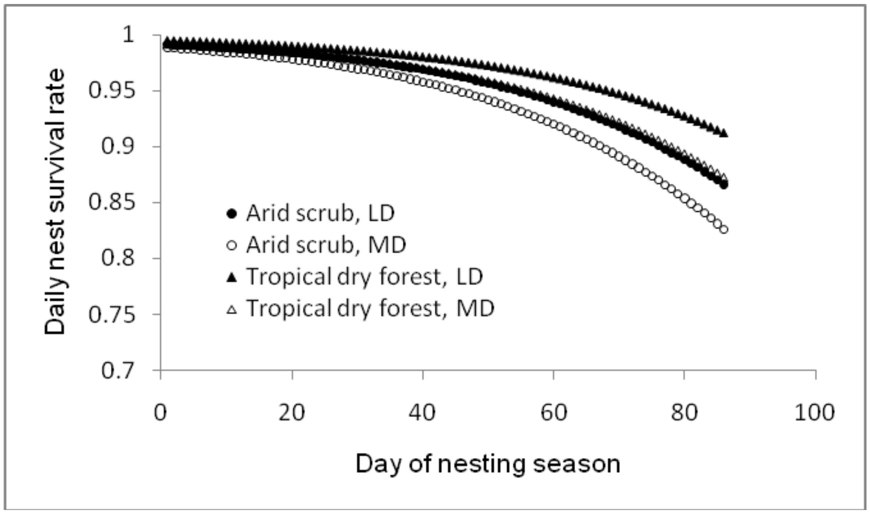

Table 7. Model selection results for daily nest survival for open cut nests in less and more disturbed arid scrub and tropical dry forest vegetation in Machalilla National Park, Ecuador in 2008 and 2009.

Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Parameters	Deviance
$S_{\text{(T+veg type+year+plant)}}$	2325.09	0	0.9881	1	7	2311.077
$S_{\text{(T+veg type+year+stage)}}$	2336.602	11.5119	0.0031	0.0032	9	2318.581
$S_{\text{(T+veg type+year)}}$	2336.83	11.7397	0.0028	0.0028	6	2324.82
$S_{\text{(TT+veg type+year)}}$	2337.758	12.6679	0.0018	0.0018	7	2323.745
$S_{\text{(T+veg type+year+height)}}$	2338.169	13.0796	0.0014	0.0014	7	2324.157
$S_{\text{(T+veg type+year+weeds/shrubs)}}$	2338.22	13.1303	0.0014	0.0014	7	2324.207
$S_{\text{(T+veg type+year+cover)}}$	2338.247	13.1573	0.0014	0.0014	7	2324.234
$S_{\text{(veg type+year)}}$	2378.517	53.4267	0	0	5	2368.51
$S_{\text{(year)}}$	2389.95	64.8603	0	0	2	2385.949
$S_{\text{(veg type)}}$	2391.946	66.8561	0	0	4	2383.941
$S_{(.)}$	2417.041	91.9516	0	0	1	2415.041

Table 8. Beta estimates and 95% confidence intervals for parameters in the best model for open cup nests in less and more disturbed arid scrub and tropical dry forest vegetation in Machalilla National Park, Ecuador in 2008 and 2009.

Parameter	β Estimate	SE	Lower 95% CI	Upper 95% CI
b0	30.2610	3.5462	23.3105	37.2115
Linear time*	-0.2821	0.0446	-0.3695	-0.1948
Year*	0.3827	0.1629	0.0634	0.7019
Plant spiny or not*	0.4702	0.1657	0.1455	0.7950
Arid scrub LD*	0.8589	0.2018	0.4633	1.2545
Arid scrub MD	-0.0097	0.1409	-0.2859	0.2666
Tropical dry forest LD	0.1828	0.2122	-0.2330	0.5987

Figure 3. Daily nest survival rate of open cup nests as the nesting season progressed in less disturbed (LD) and more disturbed (MD) arid scrub and tropical dry forest in 2008 and 2009 combined.

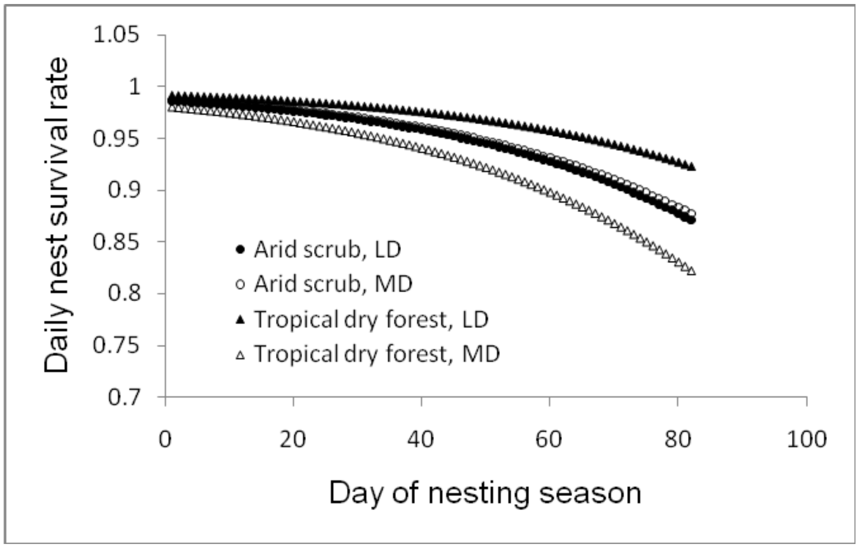

Table 9. Model selection results for daily nest survival for enclosed nests in less and more disturbed arid scrub and tropical dry forest vegetation in Machalilla National Park, Ecuador in 2008 and 2009.

Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Parameters	Deviance
$S_{(T+year+stage)}$	594.5269	0	0.4400	1	6	582.5086
$S_{(T+year+plant)}$	596.9565	2.4296	0.1306	0.2968	4	588.9478
$S_{(T+year)}$	596.9692	2.4423	0.1298	0.2949	3	590.964
$S_{(T+year+height)}$	597.3554	2.8285	0.1070	0.2431	4	589.3467
$S_{(TT+year)}$	597.6167	3.0898	0.0939	0.2133	4	589.608
$S_{(T+year+cover)}$	598.8627	4.3358	0.0504	0.1144	4	590.8539
$S_{(T+year+weeds/shrubs)}$	598.9407	4.4138	0.0484	0.11	4	590.932
$S_{(year)}$	619.8208	25.2939	0	0	2	615.8182
$S_{(veg\ type+year)}$	623.3783	28.8514	0	0	5	613.3652
$S_{(.)}$	624.8846	30.3577	0	0	1	622.8837
$S_{(veg\ type)}$	625.7205	31.1936	0	0	4	617.7118

Table 10. Beta estimates and associated 95% confidence intervals for the best model for enclosed nests.

Parameter	β Estimate	SE	Lower 95% CI	Upper 95% CI
b0	54.6809	3.5390	47.7444	61.6174
Linear time*	-0.3366	0.0679	-0.4697	-0.2034
Year	0.3998	0.2858	-0.1604	0.9600
Construction stage*	-0.6676	0.2458	-1.1493	-0.1858
Laying stage	-0.5910	1.0391	-2.6276	1.4455
Incubating stage	-0.8747	0.5489	-1.9506	0.2012
Plant	-0.3598	0.2616	-0.8726	0.1530
Height	0.0462	0.0366	-0.0254	0.1179

Figure 4. Daily nest survival rate of enclosed nests as the nesting season progressed in less disturbed (LD) and more disturbed (MD) arid scrub and tropical dry forest in 2008 and 2009 combined.

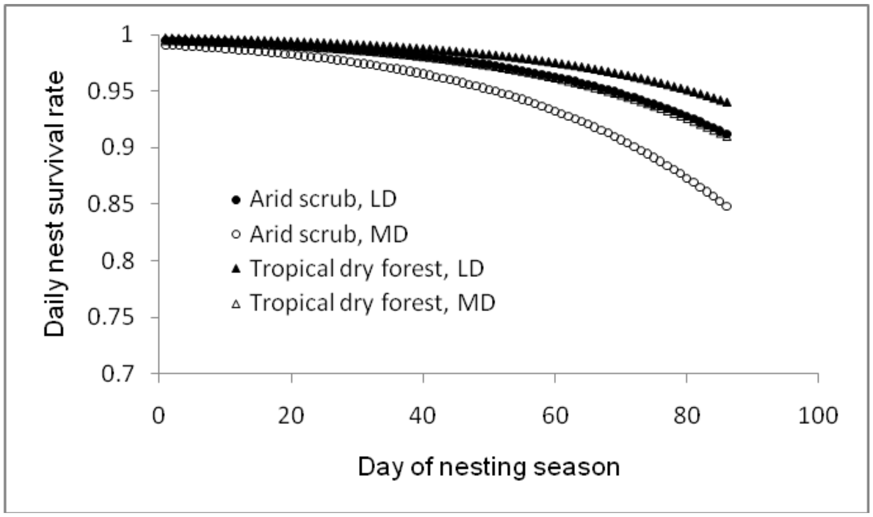

Table 11. Model selection results for daily survival rate of white-tipped dove nests in less and more disturbed tropical dry forest vegetation in Machalilla National Park, Ecuador in 2008 and 2009.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Parameters	Deviance
$S_{(T+veg\ type+year+stage)}$	224.6838	0	0.9099	1	8	208.5222
$S_{(veg\ type+year)}$	230.6511	5.9673	0.0145	0.0506	5	220.584
$S_{(T+veg\ type+year)}$	231.7151	7.0313	0.0262	0.0297	6	219.621
$S_{(year)}$	232.2882	7.6044	0.0196	0.0223	2	228.2748
$S_{(veg\ type)}$	232.8297	8.1459	0.0150	0.017	4	224.785
$S_{(TT+veg\ type+year)}$	233.2459	8.5621	0.0122	0.0138	7	219.1203
$S_{(.)}$	236.3504	11.6666	0.0026	0.0029	1	234.346

Table 12. Beta estimates and associated 95% confidence intervals for nests of white-tipped doves in less (LD) and more disturbed (MD) tropical dry forest in 2008 and 2009.

Parameter	β Estimate	SE	Lower 95% CI	Upper 95% CI
b0	194.2151	0	194.2151	194.2151
Arid scrub LD	0.621258	0.8489	-1.04251	2.2850
Arid scrub MD	-1.61606	0.8926	-3.36565	0.1335
Tropical dry forest LD*	0.870654	0.4339	0.02019	1.7211
Linear time	-0.03353	0.1448	-0.31742	0.2504
Year	0.5608	0.4997	-0.41866	1.5403
Construction*	-17.4663	0	-17.4663	-17.4663
Laying*	-17.2358	0	-17.2358	-17.2358
Incubating*	-16.2925	0	-16.2925	-16.2925

Figure 5. Daily nest survival rate of white-tipped dove nests as the nesting season progressed in less disturbed (LD) and more disturbed (MD) tropical dry forest in 2008 and 2009 combined.

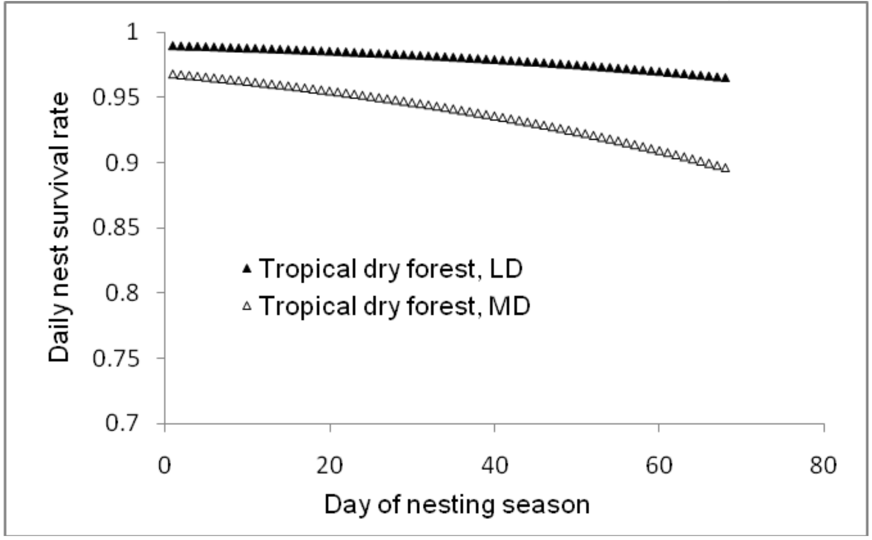

Table 13. Model selection results for daily survival rate of crimson-breasted finch nests in less and more disturbed arid scrub vegetation in Machalilla National Park, Ecuador in 2008 and 2009.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
$S_{(T+veg\ type+year)}$	1320.3461	0	0.5942	1	6	1308.3334
$S_{(TT+veg\ type+year)}$	1321.9107	1.5646	0.2718	0.4574	7	1307.8938
$S_{(T+veg\ type+year+stage)}$	1323.3248	2.9787	0.1340	0.2255	9	1305.2976
$S_{(veg\ type+year)}$	1375.7394	55.3933	0	0	5	1365.7303
$S_{(year)}$	1382.2146	61.8685	0	0	2	1378.2128
$S_{(veg\ type)}$	1427.949	107.6029	0	0	4	1419.943
$S_{(.)}$	1444.2328	123.8867	0	0	1	1442.2322

Table 14. Beta estimates and associated 95% confidence intervals for crimson-breasted finch nests in less (LD) and more disturbed (MD) arid scrub and tropical dry forest in 2008 and 2009.

Parameter	β Estimate	SE	Lower 95% CI	Upper 95% CI
b0	72.5470	8.0111	56.8453	88.2487
Linear time*	-0.9062	0.1205	-1.1425	-0.6610
Year	-0.6055	0.3147	-1.2224	0.0114
Arid scrub LD	-0.0845	0.4490	-0.9646	0.7955
Arid scrub MD	-0.3845	0.4438	-1.2543	0.4854
Tropical dry forest LD	1.0023	0.6242	-0.2210	2.2257

Figure 6. Daily nest survival rate of the crimson-breasted finch as a function of day of the nesting season, in less disturbed (LD) and more disturbed (MD) arid scrub vegetation in 2008 and 2009.

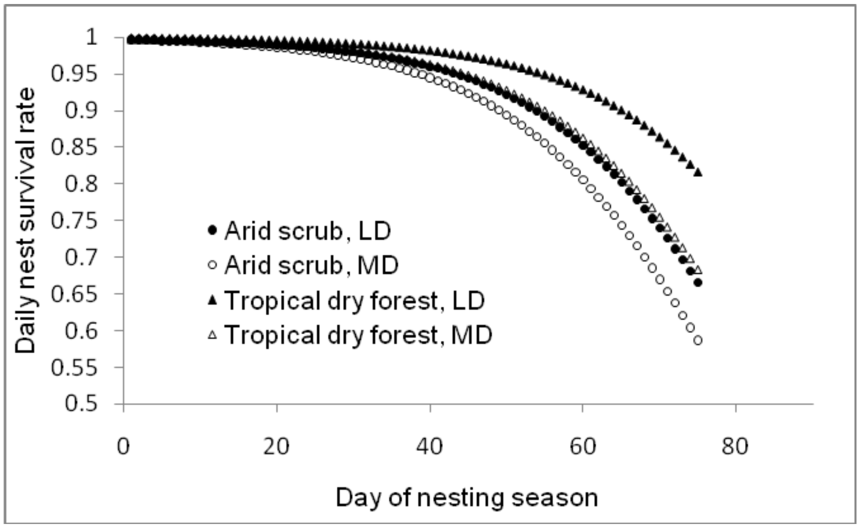

Table 15. Model selection results for daily survival rate of necklaced spinetail nests in less and more disturbed arid scrub and tropical dry forest vegetation in Machalilla National Park, Ecuador in 2008 and 2009.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
$S_{(T+year)}$	357.8705	0	0.4265	1	3	351.8622
$S_{(T+year+stage)}$	358.6106	0.7401	0.2946	0.6907	5	348.5899
$S_{(TT+year)}$	358.7227	0.8522	0.2785	0.6531	4	350.7089
$S_{(year)}$	372.9712	15.1007	0.0002	0.0005	2	368.9671
$S_{(veg\ type+year)}$	374.197	16.3265	0.0001	0.0003	5	364.1763
$S_{(.)}$	381.3312	23.4607	0	0	1	379.3298
$S_{(veg\ type)}$	382.2739	24.4034	0	0	4	374.2602

Table 16. Beta estimates and associated 95% confidence intervals for necklaced spinetail nests in less (LD) and more disturbed (MD) tropical dry forest in 2008 and 2009.

Parameter	β Estimate	SE	Lower 95% CI	Upper 95% CI
b0	50.3578	3.8917	42.7301	57.9855
Linear time*	-0.3374	0.0830	-0.5000	-0.1747
Year*	1.2790	0.4062	0.4828	2.0752

Figure 7. Daily nest survival rate of the necklaced spinetail as a function of day of the nesting season, in less disturbed (LD) and more disturbed (MD) arid scrub and tropical dry forest vegetation in 2008 and 2009 combined.

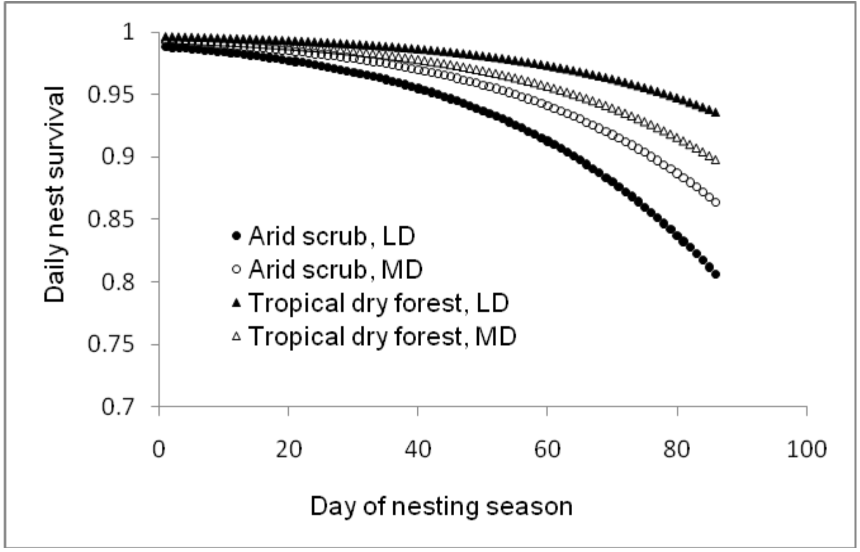

Table 17. Model selection results for daily survival rate of croaking ground-dove nests in less and more disturbed arid scrub vegetation in Machalilla National Park, Ecuador in 2008 and 2009.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
$S_{(TT+veg\ type+stage)}$	351.5641	0	0.9759	1	8	335.4269
$S_{(TT+veg\ type)}$	361.3035	9.7394	0.0075	0.0077	5	351.2464
$S_{(veg\ type)}$	361.4776	9.9135	0.0069	0.007	3	355.4548
$S_{(T+veg\ type)}$	363.0537	11.4896	0.0031	0.0032	4	355.0157
$S_{(veg\ type+year)}$	363.1621	11.598	0.0030	0.003	4	355.1242
$S_{(.)}$	363.5926	12.0285	0.0024	0.0024	1	361.5888
$S_{(year)}$	364.8138	13.2497	0.0013	0.0013	2	360.8024

Table 18. Beta estimates and associated 95% confidence intervals for nests of croaking ground-doves in less and more disturbed arid scrub vegetation in Machalilla National Park, Ecuador in 2008 and 2009.

Parameter	β Estimate	SE	Lower 95% CI	Upper 95% CI
b0	52.1597	20.5665	11.8493	92.4701
Linear time	-1.1695	0.7554	-2.6501	0.3111
Quadratic time	0.1155	0.0877	-0.0564	0.2874
Arid scrub LD	-0.9428	0.6599	-2.2361	0.3505
Arid scrub MD	1.0951	0.7186	-0.3135	2.5036
Tropical dry forest LD	-0.1	1598.245	-3132.66	3132.459
Construction	-1.0338	1.0717	-3.1343	1.0667
Laying	-0.5215	0.9299	-2.3442	1.3012
Incubating	1.1793	0.8451	-0.4771	2.8358

Figure 8. Daily nest survival rate of the croaking ground-dove as a function of day of the nesting season, in less disturbed (LD) and more disturbed (MD) arid scrub vegetation in 2008 and 2009 combined.

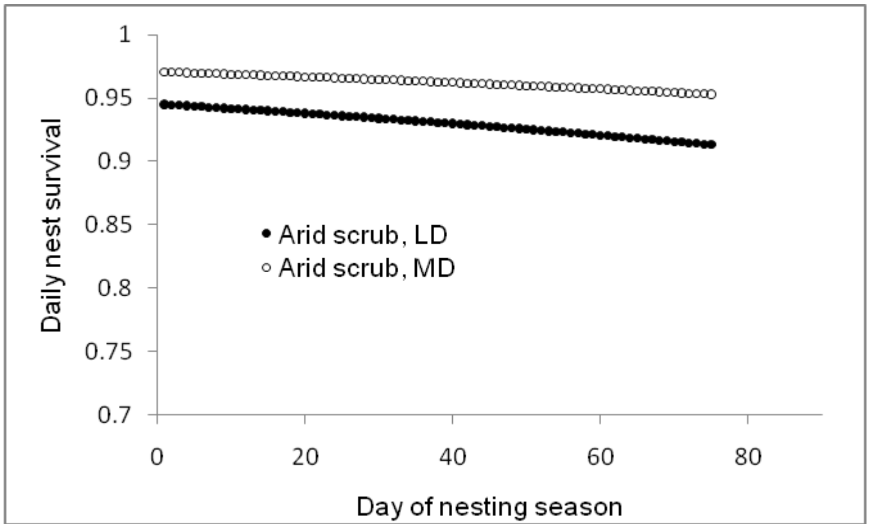

Table 19. Model selection results for daily survival rate of southern yellow-grosbeak nests in less and more disturbed arid scrub and tropical dry forest vegetation in Machalilla National Park, Ecuador in 2008 and 2009.

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Parameters	Deviance
$S_{(\text{T+veg type+year+stage+height+cover})}$	188.0985	0	0.9315	1.0000	11	165.8032
$S_{(\text{T+veg type+year+ height+cover})}$	194.4794	6.3809	0.0383	0.0412	8	178.3189
$S_{(\text{T+veg type+year+cover})}$	196.8324	8.7339	0.0118	0.0127	7	182.7077
$S_{(\text{T+veg type+year+stage})}$	198.0686	9.9701	0.0064	0.0068	9	179.8677
$S_{(\text{T+veg type+year+height})}$	198.2337	10.1352	0.0059	0.0063	7	184.109
$S_{(\text{T+veg type+year+plant})}$	200.136	12.0375	0.0023	0.0024	7	186.0113
$S_{(\text{T+veg type+year})}$	200.2476	12.1491	0.0021	0.0023	6	188.1542
$S_{(\text{TT+veg type+year})}$	202.2287	14.1302	0.0008	0.0009	7	188.1039
$S_{(\text{veg type})}$	203.3273	15.2288	0.0005	0.0005	4	195.2829
$S_{(\text{veg type+year})}$	203.8874	15.7889	0.0004	0.0004	5	193.8207
$S_{(.)}$	206.5034	18.4049	0.0001	0.0001	1	204.499
$S_{(\text{year})}$	208.1533	20.0548	0.00004	0	2	204.1401

Table 20. Beta estimates and associated 95% confidence intervals for nests of southern yellow-grosbeaks in less (LD) and more disturbed (MD) arid scrub and tropical dry forest.

Parameter	β Estimate	SE	Lower 95% CI	Upper 95% CI
b0	38.1791	20.3695	-1.7450	78.1033
Linear time*	-0.6786	0.2715	-1.2107	-0.1466
Arid scrub LD*	1.4820	0.7484	0.0151	2.9489
Arid scrub MD*	2.9405	0.8682	1.2388	4.6423
Tropical dry forest LD	1.0675	0.8622	-0.6225	2.7574
Year	-0.1510	0.8690	-1.8543	1.5522
Cover*	-0.5439	0.2356	-1.0056	-0.0822
Height*	0.4696	0.1724	0.1318	0.8074
Construction	-0.9146	0.9980	-2.8706	1.0413
Laying	-1.8581	1.0132	-3.8438	0.1277
Incubating	0.5722	0.8627	-1.1186	2.2631

Figure 9. Daily nest survival rate of the southern yellow-grosbeak as a function of day of the nesting season, in less disturbed (LD) and more disturbed (MD) arid scrub and tropical dry forest vegetation in 2008. Patterns for 2009 were nearly the same although less extreme, and thus are not shown.

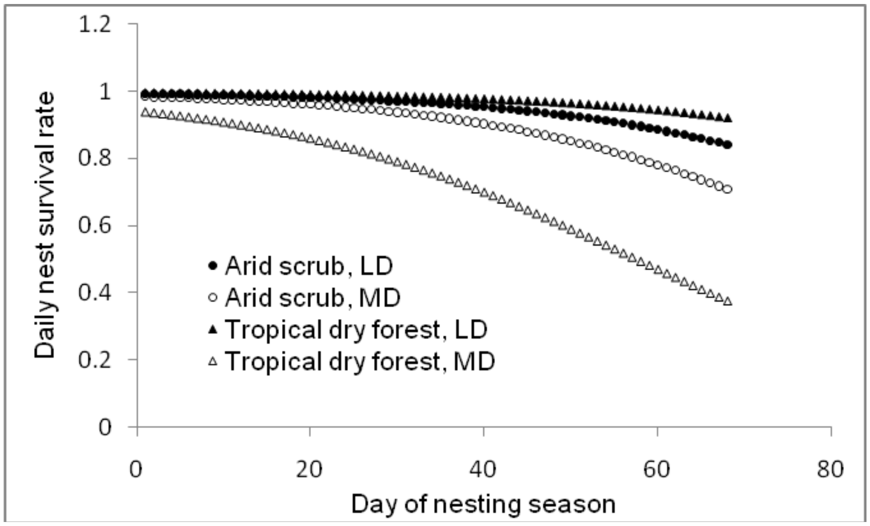

Table 21. Estimates of productivity for each of the five species with large sample sizes, pooled across 2008 and 2009. Total numbers of chicks successfully fledged are shown in parentheses.

Vegetation type	CBFI	CGDO	NEST	SYGB	WTDO
Arid scrub, LD	0.4697 (128)	0.0777 (16)	0.1361 (38)	0.6739 (17)	N/A
Arid scrub, MD	0.2363 (81)	0.0921(21)	0.2094 (58)	0.6533 (17)	N/A
Tropical dry forest, LD	0.1871 (16)	N/A	0.4863 (136)	0.4935 (19)	0.6667 (15)
Tropical dry forest, MD	0.1180 (9)	N/A	0.2195 (40)	0	0.4171 (22)

Chapter 5 - Breeding records of birds from the Tumbesian region of Ecuador

Introduction

Little is known about the reproduction of many species of tropical birds, and especially those endemic to limited geographic regions. Despite several existing publications on the nesting biology of birds in southwestern Ecuador (Marchant 1958, 1959, 1960, Balchin 1996, Best et al. 1996), basic information such as clutch size, egg descriptions, incubation and nestling times and nest and site characteristics are unknown for many species. This information not only allows the examination of regional and local variation in these traits within species, but can be crucial to conservation efforts which aim to increase reproductive success of threatened species. For example, the predation risk of a nest and the normal development of the embryo and nestlings are strongly influenced by the nest structure and location as well as the behavior of the adults (Gill 1990). Further, clutch size differences can reflect the energy available for egg formation and the lifetime reproductive success (Gill 1990). Incubation periods reflect the egg size, adult weight, and probability of predation; while nestling periods are influenced by food quantity and quality and temperature; and both can vary greatly within species (Gill 1990). Nest–site selection is an integral component of habitat selection and may influence the evolution of other aspects of the morphology and behavior of a species (Gill 1990, Stauffer and Best 1986).

The Tumbesian region of south–western Ecuador and north–western Peru encompasses the great majority of remaining coastal tropical dry forest in South America, and is one of the most threatened bioregions in the world due to heavy human–use in the form of development and livestock grazing (Best and Kessler 1995). The region, home to 32 threatened or near threatened bird species and 61 endemic bird species, has already lost over 95% of its original forest and is extremely vulnerable to continued habitat fragmentation and heavy grazing by domesticated animals (Wege and Long 1995). Machalilla National Park is one of the largest parks in the Tumbesian region (55,095 ha), and contains 67% of its endemic bird species (Wege and Long 1995). The park has a marked gradient of rainfall caused by differences in elevation (0–860 m) and slope position relative to the coast. As a consequence, the vegetation ranges from arid scrub to humid fog forest. A majority of the endemic bird species are found in the driest vegetation types, arid scrub and tropical dry forest, which are often also the most affected by human–use. This paper presents descriptions of the nests, eggs, incubation and nestling periods and nest placement for 32 bird species found in Machalilla National Park, in the highly threatened Tumbesian region of coastal Ecuador. Fourteen of the species discussed are endemic to the Tumbesian region (marked with an asterisk in the text and Table 1), and first descriptions of part of the breeding biology of twelve species are given.

Methods

All nests described in this paper were found in either arid scrub or tropical dry forest vegetation within the boundaries of Machalilla National Park. Arid scrub consists primarily of low, bushy trees and cacti and has an average canopy height of four meters. Tropical dry forest is similar to arid scrub, but differs by having trees with diameters more than twice that of the biggest trees in arid scrub, an average canopy height of eight meters, and greater canopy density. In contrast to arid scrub, tropical dry forest riverbeds retain moisture year–round and trees growing in these areas maintain their leaves for a majority of the year. The nesting season in Machalilla National Park coincides with the rainy season, which is generally from January to April. During the rainy season the normally dry vegetation flushes green, and weedy lianas often quickly spread through the understory and cover the trees.

From mid–January to late May of 2008 and 2009 my assistants and I systematically searched for nests in two 100 ha plots in each vegetation type (arid scrub and tropical dry forest). We did not search in the more humid hills where fog forest dominates. Both 2008 and 2009 had similar rainy season, although in 2008 there was more rainfall, especially in the hills, causing the riverbeds to fill more frequently and for longer periods. Once a nest was found, its location was marked with a GPS and visited every two to three days (more frequently closer to hatching or fledging dates) to check the status of the eggs or chicks or to note cause–specific nest failure. High nests were reached using a six meter ladder. Enclosed nests were monitored either by creating a small hole in the side of the nest (which was often quickly repaired by the parents) or by making careful observations of parental behavior and nestling noises. When possible, eggs were carefully removed from the nest, measured with an electronic caliper and photographed. Note that nest success data will be presented in subsequent publications.

Clutch sizes given are estimated only from nests where eggs were seen in active nests over consecutive nest checks. Incubation periods given were based on estimates of the time of laying of the last egg to the hatching of the last egg; while nestling periods were estimates of the time between hatching of the last egg and fledging of the last chick from the nest. In some cases chicks may have left nests before being able to fly. Once a nest finished due to chick(s) fledging or nest failure, detailed nest placement measurements were taken following BBIRD methods (Martin et al. 1997). In a five meter radius circle centered on each nest we recorded: 1) the species, height, diameter at breast height (dbh) and crown size of the tree the nest was found in; 2) the height of the nest, its orientation on the trunk, distance to the foliage border, distance to the trunk, number of branches supporting the nest and their average diameter, and the percent of cover above the nest and in each cardinal direction; and 3) internal and external measurements of the nest, and a description of the nest materials. This information is summarized for each species in Table 1. The "first descriptions" (egg size, incubation time, etc) given in this paper are only "first" to the best of my knowledge, and I apologize if I missed the relevant citation. To determine if a piece of information I gathered had been previously published I searched the Web of Science (http://apps.isiknowledge.com), the Searchable Ornithological Research Archive (http://elibrary.unm.edu/sora), the Zoological Record (http://ovidsp.tx.ovid.com), the Handbook of the Birds of the World series (1996–2008), and numerous bird journal indices.

Results

Rufous–necked Woodrail (*Aramides axillaris*): We found two nests of this species, both within 500 m of a seasonally dry riverbed in tropical dry forest. One nest was 3.5 m high in a 6 m *Astronium graveolens*, and the other was 2.5 m high in a 5 m *Maytenus sp.* The adults were not very shy during nest checking, making species identification easy. Nests were large shallow platforms made almost entirely of *Cordia lutea* sticks, with some weeds and leaves woven in. In Trinidad nests were described as "deep twiggy bowls lined with leaves and fibers 1–7 m up in vines or bushes" (Belcher and Smooker 1934, 1937, ffrench 1991). In Mexico nests are apparently found most frequently over water (Howell and Webb 1995). Both nests we found had a final clutch size of six eggs, while in Trinidad nests had three to seven eggs (Belcher and Smooker 1934, 1937, ffrench 1991). The eggs were larger than chicken eggs and were white with a lot of specks of different shades of brown in various sizes; which is similar to eggs described in Trinidad (Belcher and Smooker 1934, 1937, ffrench 1991). Both nests were found during the laying period, and the 22 day incubation period is estimated from the time the last egg was laid to the time the nest was empty (Table 1). We never saw nestlings, as rail hatchlings are subprecocial (leave the nest immediately and are fed by the parents) (Gill 1990). To my knowledge this is the first description of the incubation period for this species.

*West Peruvian Dove** (*Zenaida meloda*): Seventy percent of the 23 nests found were in tropical dry forest and 30% in arid scrub. Nest heights ranged from 1.2–5.8 m, in 11 different tree species. *C. lutea* was used 36% of the time, *Scutia sp.* 16% of the time, *Mimosa sp.* 12% of the time, and *Geoffroea spinosa*, *Pithecellobium sp.*, *Xylosma sp.*, *Caesalpinia corimbosa*, *Armatocereus cartwrightianus*, *Jacquinia pubescens*, *Acacia rorudiana* and *Prosopis juliflora* 4% of the time each. Nests were shallow platforms of sticks from *C. lutea* and other species; similar to but smaller than those of the woodrails. The eggs were white and clutch size was always two. Incubation times ranged from 13–15 days and nestling times from 11–15 days. Marchant (1960) found two nests in southwestern Ecuador, about 90 km south of our field site on the Santa Elena Peninsula (all subsequent references from Marchant also come from this site); both were 1.5 m high and made from *C. lutea* sticks. To my knowledge this is the first description of the incubation and nestling periods of this species.

*Croaking Ground–dove** (*Columbina cruziana*): Ninety four percent of the 63 nests found were in arid scrub and 6% in tropical dry forest. The doves nested in a total of 13 different plant species. They used *C. lutea* as their nesting tree 71% of the time, *Mimosa sp.* 9% of the time, *P. juliflora* 6% of the time, *Capparis heterophylla* 4% of the time, *C. corimbosa*, *A. cartwrightianus* and *Bursera graveolens* 3% of the time each, and *J. pubescens* only once. Marchant (1960) also found that over a 4 year period the ground–doves chose *C. lutea* as their nesting tree more frequently than any other species. Nest height ranged from 0.6–4.8 m and averaged 2.5 m, while Marchant (1960) found nest height averaged 1.7 m for 297 nests. Nests were shallow, flattened cups made from small sticks, dry vines and weeds, leaves, leaf veins, feathers, grass, and cactus spines. The doves sometimes glued the nest to the branch with their feces, and the rims of the nests often became covered in feces as the chicks grew. Green weeds and leaves were woven into the outside of the nests to help camouflage them. The eggs were plain white, and clutch size was always two—although clutches of one and three eggs have been described (Marchant 1960). The incubation time ranged from 12–15 days, and the nestling period from 10–12 days. Marchant (1960) describes an incubation period of around 14 days and nestling periods around 10 days.

White–tipped Dove (*Leptotila verreauxi decolor*): Eighty nine percent of the 55 nests were found in tropical dry forest and 11% in arid scrub. The doves nested in 14 different plant species, using *C. lutea* 44% of the time, *P. juliflora* 19% of the time, *Scutia sp.* 8% of the time, *Malpighia punicifolia* and *Pithecellobium sp.* 6% of the time each, unknown species 3% of the time, and *G. spinosa*, *Guapira sp.*, *Xylosma sp.*, *Coccoloba sp.*, *Mutingia calabura*, *Ipomea carnea*, and *C. corimbosa* 2% of the time each. Nest heights ranged from 1–11 m. The majority of the nests Skutch (1981) found in Costa Rica were 1–2 m high (although rarely up to 6 m), and in Trinidad nests were usually placed around 6 m high in a palm or other tree (ffrench 1991). Wetmore (1968) occasionally found nests on the ground in Panama. Nests were very similar to those of the West Peruvian Doves, and were constructed almost entirely of small sticks from various tree species. Lichen was sometimes affixed to the outside of the nest. In Costa Rica nests were made from twigs, straws, dry grasses, weed stems, dry vine pieces, fern fragments and rootlets (Skutch 1964, 1981); while in Trinidad nests were made from small twigs and lined with fine grass (ffrench 1991). The eggs were white and the clutch size was always two. The incubation period ranged from 12–14 days, and the nestling period from 10–15 days. In Costa Rica the incubation period was 14 days, and the nestling period 15–18 days (Skutch 1981). In Trinidad the incubation period was 14–15 days and nestling period 13–14 days (ffrench 1991).

Gray–capped Cuckoo (*Coccyzus lansbergi*): Fifty percent of the 22 nests were found in tropical dry forest and 50% in arid scrub. The cuckoos nested in nine different tree species, choosing *C. lutea* 38% of the time, *Mimosa sp.* 17% of the time, *J. pubescens* and *Scutia sp.*10% of the time each, and *A. cartwrightianus*, *Coccoloba sp.*, *B. graveolens*, and *Pithecellobium sp.* 5% of the time each. The nests were usually very well hidden by foliage in all directions, and resembled those of the White–tipped and West Peruvian doves. Nest height ranged from 0.4–5 m. Marchant (1960) found three nests, ranging in height from 1.2–2 m. Nest material consisted almost entirely of sticks of *C. lutea*, although sometimes sticks from spiny plants such as *Pithecellobium sp.* were included. The eggs were large and white, and appeared very similar to those of the White–tipped and West–Peruvian doves, although the clutch size ranged from two to five with an average of 3.7 eggs. This differs from Marchant’s (1960) description of a clutch size of two to three, and his description of the eggs as greenish–white with rough chalky shells. We observed an incubation period ranging from 9–12 days, and a nestling period of 9–12 days.

Marchant (1960) speculated that the nestling period was 8–13 days. As far as I am aware, the incubation and nestling periods for this species had not been previously described.

Short–tailed Woodstar (*Myrmia micrura*): We found one nest in arid scrub, woven precariously to attach in one place 1.5 m up the stem of an unknown species of weed. The stem with the nest swung up and down in the wind, nearly tipping the tiny eggs out. The nest was a tiny cup made almost entirely of the very soft, cotton–like seed down of *I. carnea* or *Eriotheca ruizii* with small brown seeds and lichen affixed to the outside. The nest had two tiny white eggs which were shaped in elongated ovals, similar to jelly beans. The female was very aggressive towards us while we were near the nest. After observing the nest for 12 days the eggs disappeared—there was no trace of them in the nest or on the ground—making it impossible to determine exact incubation or nestling periods. Marchant (1960) provides similar descriptions of the nest and eggs of this species, as well as incubation and nestling periods. However, to my knowledge this paper provides the first published egg measurement for this species (Table 1).

*Necklaced Spinetail** (*Synallaxis stictothorax stictothorax*): Seventy two percent of the 117 nests found were in tropical dry forest, and 28% were in arid scrub. All but four nests we found were in spiny trees or cactus, and nest height ranged from 2–12 m. The spinetails chose *J. pubescens* 26% of the time, *P. juliflora* 20% of the time, *Scutia sp.* and *A. cartwrightianus* 15% of the time each, *Mimosa sp.*, *Zizyphus thyrsiflora* and *Pithecellobium sp.* 5% of the time each, *M. punicifolia* and *C. lutea* 4% of the time each, and *Morisonia americana* once. Nests were enclosed with a side tunnel entrance, and woven very tightly from the spiny sticks of nine different plants. The inside cup was lined with feathers and the soft seed down of *I. carnea* or *E. ruizii*. These descriptions are similar to Marchant's (1960). In the nest measurements given (Table 1), external diameter refers to the longest (horizontal or vertical) part of the nest, while external height refers to the perpendicular measurement. We made small holes in the sides of 18 nests to view the contents (with some difficulty due to the tightly woven, thick nest walls) (Fig. 1). We did not open more nests because we did not want to cause nest abandonment or predation, and nests were often too high or in very spiny plants. In all cases the parents quickly repaired nests we had opened. All nests but one that we opened had a clutch size of three. Marchant (1960) opened one nest that had three eggs, "lying on a lining of yellowish mossy material." We found the eggs to be small and white with a few brown spots (Fig. 1), while Marchant (1960) describes them as pure white. For all other nests we made frequent careful observations of parental activity, but it was difficult to determine the stage of the nests. Parents often entered the nests with food, but they may have been feeding the incubating parent. Based on one nest that we opened every 2–3 days, the incubation period seems to be around 25 days. The nestling period seemed to range from 16–22 days, based on opened nests or nests where we heard chicks crying. To my knowledge this is the first description of the incubation and nestling periods for this species.

Collared Antshrike (Sakesphorus bernardi bernardi)*: Eighty five percent of 26 nests were found in tropical dry forest and 15% in arid scrub. Nests were found in a total of 13 different plant species; 28% in *C. lutea*, 16% in *P. juliflora*, 8% each in *J. pubescens, Scutia sp.*, *Xylosma sp.* and *Pithecellobium sp.*, and 4% each in *Croton riviniaefolius*, *Acnistus arborescens*, *B. graveolens*, *Musa paradisiaca*, *Maytenus octogona*, and *A. graveolens*. Nests were deep cups woven to hang from bifurcating twigs or branches, and ranged in height from 1–9 m, with an average of 3 m. Marchant (1960) found the average height for 11 nests was 1.4 m. The antshrikes occasionally wove the nests so thinly that the contents were visible from the outside, though this was the minority of cases. Nest material included small twigs, dry vines and weeds, and roots on the outside of the cup, and mostly black lichen on the inside. Marchant (1960) described nests as neatly woven from dead grasses and plant stems without lining so contents were visible from the outside. The eggs were white with dark purple splotches, concentrated around the thicker end, and tiny dark purple dots all over, which is similar to Marchant's (1960) description. Clutch size was usually three, but ranged from one to three eggs. The incubation period ranged from 11–15 days, and the nestling period from 9–17 days. Marchant (1960) found the incubation period to be 15 days and the nestling period to be 11 days. Although he found only females incubating, I frequently observed males incubating.

Plain Antvireo (*Dysithamnus mentalis aequatorialis*): All three nests were found in tropical dry forest. Two nests were in *C. polyantha*, and the third in *M. americana*. The cup nests were very similar to those of the antshrikes, though smaller. Nest height ranged from 1–1.4 m. The nests were woven to hang in the fork of two small branches, and were made from flexible dry vines, plant fibers and small twigs, and were often transparent; especially the top part where the head of the incubating parent was visible. The clutch size was two or three, and the eggs were cream–colored with many large maroon splotches. These descriptions are similar to descriptions of nests in Mexico, Costa Rica and Trinidad (Skutch 1969, ffrench 1991, Howell and Webb 1995). The incubation period was around 10 days, and the nestling period around 11 days. In Costa Rica the incubation and fledging periods were 15 and 9 days, respectively (Skutch 1969).

*Elegant Crescentchest** (*Melanopareia elegans*): All three nests were found on the ground in arid scrub, and blended in perfectly. We only discovered them by stepping close enough to flush the parent. The nests were enclosed except for a small side entrance, and made almost entirely from dry strips of cactus and dry weeds (Fig. 2). The clutch size was three, and the eggs were light blue with large brown spots at the wider end (Fig. 2). All the nests were found close to or during the nestling stage, making determining the incubation period impossible. The nestling period appeared to be around 10–12 days. To my knowledge this is the first nest and egg description for this species.

Southern Beardless–Tyrannulet (*Camptostoma obsoletum sclateri*): Eighty one percent of 43 nests were found in tropical dry forest and 19% in arid scrub. Forty nine percent of the nests were found in *P. juliflora*, 11% in *C. lutea*, 9% each in *Scutia sp.* and *J. pubescens*, 6% each in *C. heterophylla*, *Pithecellobium sp.* and unknown species, and 1% each in *Sapindus saponaria*, *M. calabura*, *Z. thyrsiflora* and *Mimosa sp*. Nest height ranged from 2.6–11 m. In southwestern Ecuador and Trinidad nests ranged in height from 1–4 m (Marchant 1960, ffrench 1991), while in Costa Rica heights ranged from 1.5–9 m (Skutch 1981). The nests were globular with a small entrance hole at the top or side. We were able to knock down a few nests after the chicks had fledged to examine the material used; they consisted mostly of small sticks, feathers, and dry algae from the riverbed, as well as lichen, leaves, small strips of a plastic rice bag, and spider web. The inside cup was lined with the soft cotton–like seed down of *E. ruizii*. This is similar to the description given of nests in Suriname by Haverschmidt (1968). The nests were most often very high and were always within 1 m of active wasp nests (as Marchant (1960) and ffrench (1991) also found), making them difficult to check. We made careful observations of parental behavior and noted nestling noises, but could not report exact incubation or nestling periods. Parents were very shy, and only arrived to the nest if the observer was still and at least 10 m from the nest. Marchant (1960) gives descriptions of the eggs, incubation and nestling periods.

*Tumbesian Tyrannulet** (*Phaeomyias tumbezana*): We found one nest 3.5 m up in an *A. rorudiana* tree in arid scrub vegetation. Marchant (1960) found 11 nests with an average height of 2.4 m. The small cup nest was suspended from the fork of small twigs, and made of leaf veins, the soft cotton–like seed down of *I. carnea* or *E. ruizii,* feathers and tiny sticks. The nest was too high and delicate to try to remove the eggs for description and measurement. The nest was found with two eggs, and after seven days the chicks hatched. Thus, we were unable to determine the total incubation period. The parents were not shy during the nestling period, and brought food to the chicks every few minutes. We estimated the nestling period to be 10 days, although Marchant (1960) found it to be 14–15 days. Marchant (1960) also describes the eggs and incubation periods of this species.

Yellow–olive Flatbill (*Tolmomyias sulphurescens*): We found one nest of this species in tropical dry forest, hanging 2.5 m from the ground on the limb of a *Xylosma sp.* tree. Nests in Trinidad were found to range from 2–12 m high, and in Costa Rica from 2–7 m high (Skutch 1960, ffrench 1991). The nest was made of dry, course, straw–like grasses; weeds and bark, and was lined with the soft seed down of *E. ruizii*. Unlike descriptions given for the species in Costa Rica, Trinidad and Mexico, the nest was not made primarily of dark hair–like fibers (Skutch 1960, ffrench 1991, Howell and Webb 1995). The nest was elongated vertically and enclosed, with a tube entrance coming up from the bottom of the nest, and was much larger than the 25 x 13 cm nests described in Trinidad (ffrench 1991, Table 1). We had to make a small hole in the side to view the contents, but unfortunately the parents abandoned it afterwards and we were unable to determine incubation or nestling periods. There were two light tan–colored eggs in the nest, with small brown spots clustered mostly at the thicker end; which is similar to what others have observed (Skutch 1960, ffrench 1991, Howell and Webb 1995). Skutch (1960) gives incubation and nestling periods for Costa Rican birds.

Tawny–crowned Pygmy–tyrant (*Euscarthmus meloryphus*): Eighty six percent of the 14 nests we found were in arid scrub and 14% in tropical dry forest. The nests were found in a total of five different plant species; *C. lutea* 54% of the time, *Guapira sp.* 13% of the time, and *C. corimbosa*, *P. juliflora*, and an unknown species 8% of the time each. Nest height ranged from 0.4–4 m. Marchant (1960) found 20 nests ranging from 0.5–1.7 m high. The small and fragile cup nests were made of tiny sticks, dry weed stems, vines, bark, grass, lichen and the soft cotton–like seed down of *I. carnea* or *E. ruizii*. Nests were well hidden in the scrub, and were often nearly transparent. Marchant (1960) gives a similar nest description. Clutch size ranged from one to three eggs, though Marchant (1960) only found nests with two eggs. The eggs were white with tiny brown spots around the middle; I did not observe any lavender spots as Marchant (1960) did. We found the incubation period to be around 11 days and the nestling period around 12 days, while Marchant (1960) lists the incubation period as 14–15 days and the nestling period 11–12 days.

Bran–colored Flycatcher (Myiophobus fasciatus): Seventy five percent of the five nests were found in tropical dry forest and 25% in arid scrub. Two nests were in the tree *Pithecellobium sp.*, and the others were in *J. pubescens*, *Scutia sp.* and *A. graveolens*. Nest height ranged from 1.5–7 m. Nests were small cups consisting of strands of dark lichen woven with dry, flexible twigs or vines, and sometimes strips of bark. In Trinidad nests were made from bark, bamboo sheaths and cobweb and lined with fine fibers or plant down (ffrench 1991). The eggs were cream–colored with dark orange spots clustered around the thicker end, and clutch size was always two; which is very similar to the description of Colombian eggs and clutch size by Sclater and Salvin (1879). ffrench (1991) gave the clutch size in Trinidad as one or two, and described the eggs as cream colored with red–brown spots forming a wreath. The incubation time was around 17 days, and the nestling period around 11 days. In Costa Rica Skutch (1960) also found the incubation period to be 17 days, but listed the nestling period as 15–17 days.

Vermillion Flycatcher (*Pyrocephalus rubinus*): All 13 nests were found in arid scrub. Ninety three percent of the nests were in *P. juliflora*, and 7% in *C. lutea*. Marchant (1960) found 200 nests over a four year period, the majority of which were in dead bushes, *C. lutea* and *Pithecellobium sp*. The nests we found were almost always in trees along dirt roads, rather than in the forest; and placed on top of branches (glued with domestic animal feces) or in a fork. The shallow cup nests were made of fine dry weeds and vines, feathers, lichen, and the seed down of *I. carnea* or *E. ruizii*. These descriptions are similar to Marchant's (1960). Nests in Colombia were made from lichen and grass and in Mexico from fine twigs, grasses and fibers (Hilty and Brown 1986, Howell and Webb 1995). Nest height ranged from 2–4 m, while the nests Marchant (1960) found ranged in height from 0.8–5.6 m. Clutch size ranged from one to three, and the eggs were white with a belt of brown spots around the middle. In Colombia and Mexico the clutch was two or three and the eggs were white with large red–brown or dark brown and gray spots (Hilty and Brown 1986, Howell and Webb 1995). The incubation period was 10–15 days and the nestling period 11–15 days. Marchant (1960) found the incubation period to be 13–14 days and the nestling period to be 13–15 days.

Black–and–White Becard (Pachyramphus albogriseus): All four nests were found in tropical dry forest and all in large trees at least 10 m tall with a dbh of at least 18 cm. Nests were found in *Ceiba trichistandra*, *P. juliflora*, *Albizia guachapele*, and *C. heterophylla* trees. Nest height ranged from 7–10 m, while in Costa Rica nests ranged from 7–20 m high (Stiles and Skutch 1989). Nests were enclosed spheres wedged in the fork of branches or the trunk, with an entrance hole on one side. They consisted of soft, flexible strips of bark and small sticks. Costa Rican nests were made of dead leaves, moss and vine bits (Stiles and Skutch 1989). The nests were too high to reach with the 6 m ladder, and thus measurements given are based on visual estimates using a tape measure (Table 1). Further, we could not obtain reliable information for incubation and nestling periods based solely on parental cues. Parents were seen adding material to the nests through the entire activity period; the longest being 40 days.

One–colored Becard (*Platypsaris homochrous*): All 25 nests were found in tropical dry forest and all in large trees; 63% in *P. juliflora*, 31% in *C. trichistandra*, and 6% in *Z. thyrsiflora*. Nests were enclosed and hung from a branch in a triangle or pear shape with a small entrance hole in the side. Nests in *P. juliflora* were almost always hanging over a seasonal riverbed, while nests in *C. trichistandra* never were. Nest height ranged from 4–14 m. Nests were primarily made of dry, straw–like grass and weeds; but vines, lichen and small sticks were also used. The inside cup of the nest was lined with feathers, dry leaves and the soft cotton–like seeds of *E. ruizii*. Nest foliage cover was much lower in all directions than the nests of most other species in this paper, likely because the nests were hanging. We made small holes in the sides of several nests to view the contents. One of the nests we opened became abandoned by the parents, and the other was repaired. One nest had three eggs and the other four. The eggs were cream–colored with many tan spots at the wider ends, which is similar to a description of Colombian eggs (Sclater and Salvin 1879). Because the nests were high and enclosed we could not determine the incubation period. The estimated nestling period was 24–29 days, based on observations of parents bringing food. The actual period may be shorter. To my knowledge incubation and nestling periods are not yet described for this species.

*Fasciated Wren** (*Campylorhynchus fasciatus*): All 15 nests were found in tropical dry forest. Thirty percent of nests were found in *P. juliflora*, 21% each in *J. pubescens* and *Z. thyrsiflora*, and 7% each in *Guazuma ulmifolia*, *A. cartwrightianus*, *Citrus reticulata* and *C. heterophylla*. Nest heights ranged from 3–6 m. Nests were enclosed and irregularly–shaped, and were often clumped with non–active or sleeping nests. The nests were principally made of straw–like dry weeds and soft strips of bark, with dry leaves and sometimes bits of human trash such as string or plastic bags. In the nest measurements given, external diameter refers to the longest (horizontal or vertical) part of the nest, while external height refers to the perpendicular measurement (Table 1). We were only able to open one nest, as most nests were too high or past the egg stage. The nest had four cream–colored eggs with tiny tan spots (Fig. 3). Although we made behavioral observations at each nest, it was nearly impossible to determine if parents were bringing food to the nest to feed nestlings or to feed the other incubating parent. In northern Peru nests were made of grass and lined with feathers and cotton, and incubation was estimated to be around 17 days (Brewer 2001). To my knowledge the eggs of this species have not been previously described.

Speckle–breasted Wren (*Thryothorus sclateri*): We found one nest on the ground in tropical dry forest, very well camouflaged in a clump of weeds. The nest was enclosed with a side entrance, and made from small sticks and vines, leaves, and lichen (Fig. 4). The nest had four white eggs, evenly covered with small brown spots (Fig. 4). After 7 days of observing the nest we found broken eggs inside and no sign of the parents; therefore we could not determine incubation or nestling periods. To my knowledge this is the first description of the nest and eggs of this species.

*Long–tailed Mockingbird** (*Mimus longicaudatus*): Fifty six percent of the 16 nests found were in arid scrub and 44% in tropical dry forest. The mockingbirds used seven different plant species for nesting; 36% in *C. lutea*, 29% in *A. cartwrightianus*, and 7% each in *P. juliflora*, *J. pubescens*, cardon, *A. rorudiana* and *Mimosa sp.* Marchant (1960) found 239 nests over a 4 year period; the majority of which were in *C. sp.*, *J. pubescens*, and *A. cartwightianus*, all of which are spiny. Nest height ranged from 1–7 m with an average of 3 m. Marchant (1960) found the average nest height to be 1.7 m. Nests were shallow cups or platforms composed of medium–sized, often spiny sticks. The cups of the nests were lined with grasses, weeds, dry leaves, or lichen. Marchant (1960) describes the lining as composed of brown rootlets, plant stems and hair. Clutch size ranged from two to six eggs, but it was impossible to tell if the eggs were laid by just one female, since several females often lay in one nest. Marchant (1960) found clutches ranging from two to five eggs. The eggs were blue with lots of brown, streaky spots; which differs greatly from Marchant's (1960) description of greenish eggs spotted and smeared with reddish–brown. However, the eggs of this genus can apparently be very variable in color (Taczanowski 1877, Marchant 1960). The incubation period ranged from 12–18 days and the nestling period from 12–15 days. Marchant (1960) found the incubation period to be 12–13 days and the nestling period to be 11–14 days.

Tropical Gnatcatcher (*Polioptila plumbea*): Seventy five percent of the 16 nests found were in arid scrub and 25% in tropical dry forest. Seventy nine percent of nests were found in *C. lutea*, and 7% each in *A. rorudiana*, *Mimosa sp.*, and *C. heterophylla*. Nest height ranged from 2.7–6.8 m. Marchant (1960) found 31 nests that ranged in height from 0.6–3.2 m, mostly in *C. lutea* and dead bushes; while in Costa Rica nest height ranged from 2–8 m (Stiles and Skutch 1989). Marchant (1960) stated that the cup nests "are often entirely conspicuous and unprotected," but all the nests we found were very well hidden; as they were very small, made in the V of two branches, were the same color as the branches, and were often even slanted in the direction of the branch. Nest material consisted mostly of dry grass and the soft, cotton–like seed down of *I. carnea* or *E. ruizii*; with some weeds, lichen, feathers, spider web, and small sticks woven in. Costa Rican nests were described as "dainty moss and lichen cups saddled on limbs"

(Stiles and Skutch 1989). The eggs were white with brown specks, and clutch size ranged from two to four; agreeing with Marchant (1960) and Stiles and Skutch (1989). The incubation period was 13–14 days, and the nestling period was 12–14 days, also agreeing with Marchant (1960).

Rufous–browed Peppershrike (*Cyclarhis gujanensis*): We found two nests of this species in tropical dry forest, both in *C. lutea*. The deep cup nests were made almost entirely from dry grass or vine, with a bit of seed down from *E. ruizii* in the cup. In Trinidad nests were made of fine roots and moss (ffrench 1991), in Panama one was found that was made almost entirely of moss (Worth, 1938), and in Costa Rica nests were made from lichen, green moss and spider's egg cases and lined with coarse vegetable material (Skutch 1967). One nest was 3 m high and the other 4.5 m high, and both nests had two eggs. In Trinidad and Costa Rica nests were usually very high, with two to three eggs (ffrench 1973, 1991, Skutch 1967). The eggs were very pointy, and were white with tiny light brown spots; similar to what Skutch (1967) found but differing from eggs described from Trinidad and Venezuela in that the eggs were white and not pinkish, and did not show any larger blotches of brown (Cherrie 1916, ffrench 1973). The incubation period was around 10 days, and the nestling period 12 days. I was unable to find any previously published information on incubation or nestling periods for this species.

Red–eyed Vireo (*Vireo olivaceus*): Sixty five percent of 17 nests were found in arid scrub and 45% in tropical dry forest. Eighty two percent of the nests were in *C. lutea*, 12% in *B. graveolens*, and 6% in *P. juliflora*. Nest height ranged from 0.8–12 m, with an average of 4.2 m. Marchant (1960) found 15 nests with an average height of 3.6 m. The small cup nests were suspended from small twigs and were usually very well–hidden in the foliage, agreeing with Marchant's (1960) observations. The nests were made from dry weeds, vines and bark; and lined with black lichen, feathers and the seed down of *E. ruizii* or *I. carnea.* Clutch size ranged from two to four, and the eggs were creamy–white with very few tiny spots; again agreeing with the observations of Marchant (1960). In Panama nests usually had two white eggs spotted blackish mostly at the larger end (Hilty and Brown 1986). The incubation time ranged from 10–16 days, and the nestling time from 10–13 days. In Costa Rica both the incubation and nestling periods were 12–14 days (Skutch 1945); while Marchant (1960) found an incubation period of 12–13 days and a nestling period of 10–11 days.

*Plumbeous–backed Thrush** (*Turdus reevei*): All five nests were found in tropical dry forest in spiny trees, often close to the trunk and very well hidden. The trees were *G. spinosa, Scutia sp.*, *C. lutea*, *Xylosma sp.* and *Tabebuia billbergii*. Nest height ranged from 3–5 m. The shallow cup nests had thick walls made of sticks and vines, with bits of lichen and dry leaves and were held together with domestic animal feces (cows or horses). The eggs were blue with lots of brown spots (Fig. 5), and clutch size ranged from three to four. Both the incubation and nestling periods ranged from 9–11 days. Best et al. (1996) found one nest of this species in the Loja province of southwestern Ecuador, composed of dry grass, fine twigs and dry leaves 2 m up in a small tree leaning over a ravine. However, to my knowledge this is the first description of the eggs, incubation and nestling period for this species.

Streaked Saltator (*Saltator striatipectus*): Half of the 22 nests found were in tropical dry forest, and half in arid scrub. The saltators used seven different tree species for nesting; 41% in *C. lutea*, 18% in *Scutia sp.*, 12% in *Mimosa sp.*, and 6% each in an unknown species, *A. graveolens, C. heterophylla* and *Guapira sp*. Nest height ranged from 1.1–6 m; very similar to nests found in Colombia (Sclater and Salvin 1879). The cup nests were messily constructed of sticks and bark on the outside, with some dry weeds and vines, lichen, and leaves. The eggs were blue with dark squiggles around the thicker ends, similar to eggs in Colombia (Sclater and Salvin

1879). The clutch size ranged from two to four, whereas in Colombia usually only two eggs were observed (Sclater and Salvin 1879). The incubation period ranged from 11–14 days and the nestling period from 12–13 days. In Costa Rica chicks fledged after 13 days (Skutch 1954).

Southern Yellow–grosbeak (*Pheucticus chrysogaster*): Sixty three percent of 43 nests were found in arid scrub and 37% in tropical dry forest. Thirty eight percent of the nests were found in *C. lutea*, 9% in *P. juliflora*, 7% in *J. pubescens*, 5% each in *C. heterophylla* and unknown species, and 2% each in *M. americana*, *Xylosma sp.*, *C. trichistandra* and *Mimosa sp.* Nest heights ranged from 1.6–11 m. Marchant (1960) found six nests ranging in height from 2.9–4.3 m. Nests were loosely constructed shallow cups placed precariously on the tops of branches, and made primarily of small sticks or weed stems with some grass and vines woven in; similar to what Marchant (1960) observed. The eggs were blue with brown streaks, and clutch size ranged from two to four; agreeing with Marchant (1960). The incubation period was 10–13 days, and the nestling period 8–13 days. Marchant (1960) found the incubation period to be 14–16 days and the nestling period to be 10–12 days.

*Parrot–billed Seedeater** (*Sporophila peruviana*): We found one nest of this species in arid scrub two meters high in a *C. lutea*. Marchant (1960) found 321 nests over a four year period in southwestern Ecuador, the majority of which were in *C. lutea* and *Pithecellobium sp*. at an average height of 1.8 m. The small and fragile transparent cup nest was made of dry vines and lichen, differing from Marchant's (1960) nests which were "nearly always of the bright brown or greenish brown, hirsute tendrils of a certain unidentified creeping or trailing plant." The nest had two white eggs with beige spots, but the eggs can apparently be very variable in appearance and the clutch size can range from one to four (Marchant 1960). Both chicks successfully fledged after we had been watching the nest for 20 days. The incubation period was at least 9 days; Marchant (1960) determined a period of 11 days. The nestling period was 11 days, agreeing with what Marchant (1960) found.

*Crimson–breasted Finch** (*Rhodospingus cruentus*): Ninety one percent of the 220 nests we found were in arid scrub, and the other 10% in tropical dry forest. The finches used nine different species for nesting; *C. lutea* 90% of the time, *M. americana* and an unknown species 2% of the time each, and *Pithecellobium sp.*, *A. arborescens, Scutia sp.*, *C. riviniaefolius, J. pubescens* and *Mimosa sp.* 1% of the time each. Marchant (1960) found that the majority of the 113 nests he found were also in *C. lutea*. Nest height ranged from 0.5–5 m, averaging 2.6 m; Marchant (1960) found an average height of 1.4 m. The small cup nests were often well covered by foliage, and the outside consisted of very fine dry vines and weeds, small sticks, leaves, tree bark, green lichen, spider web and the soft cotton–like seed down of *I. carnea* or *E. ruizii*. The inside of the cup was mostly woven with black lichen. Marchant (1960) provides a similar nest description. The clutch size ranged from one to four, and the eggs were white with a few large dark brown splotches and lots of tiny dark brown spots; similar to what Marchant (1960) observed. The incubation period ranged from 9–15 days, and the nestling period from 8–13 days. Marchant (1960) found an incubation period of 10–11 days and a nestling period of 7 to 9 days.

*Collared Warbling–finch** (*Poospiza hispaniolensis*): All eight nests were found in arid scrub. Seven of the eight nests were in *C. lutea*, and the other was in *C. heterophylla*. Marchant (1960) found 83 nests over a 4 year period in southwestern Ecuador, the majority of which were also in *C. lutea* at an average height of 1 m. The nests we found ranged in height from 0.5–3.5 m with an average of 2 m. The thick outside walls of the cup nests were made from small sticks, dry stems and bark, while the insides were lined with dried weeds, vines and lichen; differing slightly from Marchant's (1960) description of nests as formed of "dead gray grasses without special lining." The eggs were light blue with a few dark splotches at the larger ends and the clutch size ranged from one to four. Marchant (1960) found nests with two to five eggs. The incubation period was 10–13 days, and the nestling period 9–13 days. Marchant (1960) found an incubation period of 11–12 days and a nestling period of 8–9 days.

*White–edged Oriole** (*Icterus graceannae*): We found two nests of this species in tropical dry forest, one 4 m up in a *P. juliflora* tree and one 3 m up in a *Scutia sp*. Marchant (1960) found a single nest 1.8 m high. The deep cup nests were constructed from flexible dry grass or vine and weeds, similar to what Marchant (1960) observed. The nests were so thinly woven they were transparent—the eggs could be seen through the nest wall. The eggs were cream–colored with large, messy dark brown splotches mostly at the thicker end (Fig. 6). One nest was found with three eggs, but was empty after seven days of observation. The other nest was found with two half–grown nestlings that fledged after six days. I could not find descriptions of the eggs, incubation or nestling periods of this species.

*Scrub Blackbird** (*Dives warszewiczi*): All seven nests were found in tropical dry forest, and five of them in a seasonally dry riverbed. The other two were in an orchard. Three nests were in *P. juliflora*, one in *C. lutea* and one in *Citrus limon*. Nest heights ranged from 3–5 m. Nests were messy shallow cups made of fine sticks, grass, mud, weeds and bits of banana leaves. Clutch size ranged from two to three and the eggs were blue with black spots. The incubation period was around 9 days and the nestling period around 12 days. I could not find previous descriptions of the nest, eggs or incubation and nestling periods of this species.

Discussion

This paper provides descriptions of the nests, eggs, and incubation and nestling periods and nest placement of 32 species (14 of which are endemic) in this highly vulnerable region of coastal Ecuador. First observations of some or all of this information are given for 12 species. The Tumbesian region is among the five most species–rich regions of the world in terms of endemic species and, as such, it is considered a critical priority for conservation action (BirdLife International 2003). Like much of the region, Machalilla National Park suffers from continual degradation from human use, and most of the vegetation is in some stage of recovery from excessive grazing and removal of trees for charcoal production (Zambrano and Vargas 1998). Several small communities still exist within the park and residents make a living by farming goats, cattle, horses and pigs—all of which roam freely and cause considerable damage to the vegetation (pers. observ.). The majority of the plant species used for nesting and nest building were endemic to the Tumbesian region; including *C. lutea*, *C. trichistandra*, *P. juliflora*, *E. ruizii*, *Pithecellobium sp.*, *B. graveolens*, *Capparis sp.* and *C. riviniaefolius*. Several other plant species used are endangered, such as *Z. thyrsiflora* and *T. billbergii*. Continued destruction of these endemic plants for charcoal production, livestock grazing and timber will surely have negative consequences for the long–term persistence of the birds in this region.

Many species nested most frequently in *C. lutea*. This is most likely due to a combination of factors; *C. lutea* is the most common tree in arid scrub vegetation, it exhibits extensive horizontally growth and thus provides a lot of cover for nests, and because it does not usually grow more than 6 m tall nests in this species were likely easier to find than those in the crowns of taller trees. Similarly, although we found that most species have an average nest height around 3 m, this may be due to the fact that nests at this height are the easiest to find. Incubation and nestling periods varied, sometimes greatly, between nests of the same species both within the study area and between the study area and the Santa Elena Peninsula where Marchant (1960) collected his data; highlighting the fact that these periods are influenced by many factors such as food availability and temperature (Gill 1990). Many species showed very short nesting cycles, in the range of 20–30 days. As was pointed out by Marchant (1960), this is likely an adaptation to the short and uncertain rainy season in the region. While much of the information given in this paper has been previously published, it was published based on studies in areas outside of Machalilla National Park. Further, few publications include information on egg and nest sizes or nest placement (but see Marchant 1960). Obtaining natural history information on the birds in the region is especially important given the high number of endemic species and the imminent threats of climate change and further habitat destruction; and will be crucial not only for evolutionary studies but for conservation efforts as well.

Table 1. Summary of 2008 and 2009 (combined) nesting data for each species. Mean values and ranges are given. n AS = number of nests found in arid scrub vegetation; n TDF = number of nests found in tropical dry forest vegetation; EDF to LDF = earliest date to last date a nest was found; CS = mean clutch size; ES = mean egg size; INC = incubation period; NESL = nestling period; MOD = maximum number of days a nest was observed to be active (may include construction); NH = mean nest height; NTH = mean nest tree height; NTDBH = mean nest tree dbh; NDT = mean nest distance to trunk; NDFB = mean nest distance to foliage border; NED = nest external diameter; NID = nest internal diameter; NEH = nest external height; NIH = nest internal height; NI = no information; NA = not applicable; * = endemic.

Species	n AS	n TDF	EDF to LDF	CS	ES (mm)	INC	NESL	MOD	NH (m)	NTH (m)	NTDBH (cm)	NDT (m)	NDFB (m)	NED (cm)	NID (cm)	NEH (cm)	NIH (cm)
Rufous-necked Woodrail	0	2	9th-23rd Feb	6 (6-6)	43.1 x 31.6	22	NI	28	3 (2.5-3.5)	5.5 (5-6)	5 (4-6)	2.1 (1.6-2.5)	1.5 (0.8-2.2)	23.8 (23.5-24)	17.2 (17-17.4)	7.3 (7-7.5)	4.4 (4.2-4.5)
West Peruvian Dove*	7	16	4th Feb-26th Mar	2 (2-2)	NI	13-15	11-15	29	3 (1.2-5.8)	4.6 (2.5-7)	10.4 (2-73)	2.1 (0.1-6)	1.3 (0.1-2.5)	15.7 (10-30)	11.4 (8.8-15)	7 (2-20)	2.6 (1.5-4)
Croaking Ground-dove*	59	4	6th Feb-27th Mar	2 (2-2)	22 x 16.8	12-15	10-12	21	2.5 (0.6-4.8)	4.2 (1.7-7)	6.4 (2-35)	2.1 (0.1-5.5)	0.8 (0.1-2.9)	8.7 (6-11)	7.4 (6.2-9.2)	3.5 (2-4.3)	2 (0.6-3)
White-tipped Dove	6	49	4th Feb-19th Mar	2 (2-2)	NI	12-14	10-15	33	3.7 (1-11)	6.2 (2.5-13)	10.6 (2-50)	2.9 (0.2-8)	1.5 (0.1-8.5)	16 (14-20)	11.3 (8.9-13)	5.8 (2-9)	2.6 (1.4-6)
Gray-capped Cuckoo	11	11	14th Feb-17th Mar	3.7 (2-5)	NI	9-12	9-12	29	2.5 (0.4-5)	4.7 (3-7)	7.8 (2-18)	2.3 (0.04-5.8)	1.1 (0.2-4.2)	17.9 (13-25)	14.6 (9-19)	7.4 (4-13)	4.3 (3-6)
Short-tailed Woodstar	1	0	24th Mar	2	12 x 7.4	12+	NI	13	1.5	1.9	1	0.3	0	2.5	2	2	1.2
Necklaced Spinetail*	33	84	4th Feb-27th Mar	3.2 (3-4)	16.5 x 13.5	~25	16-22	60	5.8 (2-12)	7.8 (2.8-19)	17.1 (0.2-70)	1.9 (0.01-6)	1.3 (0.1-8)	35.8 (24-55)	NI	27.2 (15-40)	NI
Collared Antshrike*	4	22	29th Jan-4th Apr	2.4 (1-3)	25 x 16.9	11-15	9-17	22	3 (1-9)	6.2 (1.4-12)	8.6 (2-30)	2.5 (0.06-5.5)	0.85 (0.2-3.5)	9.5 (9-10)	6.6 (5.5-7.5)	8.9 (6.7-12)	5.3 (4.5-6.5)
Plain Antvireo	0	3	26th Feb-12th Mar	2.3 (2-3)	NI	10+	11	21	1.1 (1-1.4)	5.8 (4.4-7)	4.2 (3-5.5)	1.6 (0.5-2.4)	0.5 (0.3-0.6)	7.5 (7.4-7.6)	4.6 (4.3-4.8)	6.5 (6.5-6.5)	4.5 (4.3-4.6)
Elegant Crescentchest*	3	0	18th-20th Mar	3 (3-3)	20.9 x 16.5	NI	10-12	12	0	NA	NA	NA	NA	12.1 (11.7-12.5)	9.7 (8.8-10.5)	10 (9.6-10.3)	4.6 (4.4-4.7)
Southern Beardless-tyrannulet	8	35	5th Feb-19th Mar	2	NI	NI	12-15	36	6.5 (2.6-11)	8.8 (4-15)	18 (4-47)	3.1 (0.4-6)	0.9 (0.2-4)	8.6	6.3	10.8	7.8
Tumbesian Tyrannulet*	1	0	18th Feb	2	NI	NI	10	17	3.5	4	6	1.2	0.6	5.5	4.5	4	3.2
Yellow-olive Flatbill	0	1	10th Mar	2	20.9 x 14.6	NI	NI	16	2.5	5	4	1	0.5	25	NI	53	NI
Tawny-crowned Pygmy-tyrant	12	2	6th Feb-27th Mar	1.8 (1-3)	16.1 x 12.7	11+	12	23	1.8 (0.4-4)	3.3 (0.6-5)	2.7 (0.2-8)	0.8 (0.04-3)	0.4 (0.04-2)	5.7 (5-6.5)	4.6 (4.5-5)	4.8 (3.5-6.5)	3.2 (2.2-4)

Bran-colored Flycatcher	1	4	17th Feb-19th Mar	2	NI	~17	~11	26	3.4 (1.5-7)	6.6 (3.2-10)	6.7 (4.5-10)	2.3 (1.1-3.4)	0.7 (0.2-2)	7.5 (6-8)	5 (5-5)	6 (5.5-6.5)	5 (5-5)
Vermillion Flycatcher	13	0	29th Feb-26th Mar	2.5 (1-3)	NI	10-15	11-15	33	3.1 (2-4)	5.2 (3-7.5)	8.9 (2.5-14)	1.9 (1-5.3)	1.3 (0.4-2.3)	6.1 (5.5-6.7)	5.3 (5-5.5)	3.7 (3-4.3)	2.3 (2-2.5)
Black-and-White Becard	0	4	9th Feb-19th Mar	NI	NI	NI	NI	40	9.3 (7-10)	12.5 (10-16)	47 (18-90)	2.4 (1.5-3.2)	1.2 (0.5-2)	35 (25-45)	NI	30 (20-40)	NI
One-colored Becard	0	25	4th Feb-31st Mar	3.5 (3-4)	24.1 x 17.9	NI	24-29	44	7.6 (4-14)	12.7 (9-25)	50.7 (7-110)	4.2 (0.5-7)	0.5 (0.01-1.2)	29.2 (20-38)	NI	45 (35-60)	NI
Fasciated Wren*	0	15	9th Feb-9th Mar	4	24 x 13.5	NI	NI	61	6.2 (3-12)	9.6 (4-15)	21.6 (10-50)	6.6 (0.6-60)	1 (0.3-1.6)	55	NI	35	NI
Speckle-breasted Wren	0	1	11th Apr	4	18 x 12.5	NI	NI	7	0	NA	NA	NA	NA	15	6	13	8
Long-tailed Mockingbird*	9	7	29th Jan -30th Mar	3.5 (2-6)	25.4 x 19.6	12-18	12-15	35	3 (1-7)	5.1 (1.4-10)	10.8 (3-28)	1.5 (0.07-6.5)	0.9 (0.1-2)	15.4 (11-23)	10.6 (8-13)	10.2 (6.5-15)	6.4 (3.3-10)
Tropical Gnatcatcher	12	4	6th Feb-27th Mar	2.4 (2-4)	NI	13-14	12-14	35	4.1 (2.7-6.8)	5.5 (3.5-7.5)	6.9 (3.5-16)	1.7 (0.2-4.6)	1.5 (0.3-10)	5 (4.5-5.5)	4.2 (3.8-4.5)	3.8 (3.5-4)	2.9 (2.5-3.2)
Rufous-browed Peppershrike	0	2	25th Feb-11th Mar	2 (2-2)	24.4 x 16.4	10+	12	22	3.8 (3-4.5)	5 (5-5)	8 (8-8)	2.8 (2-3.5)	0.9 (0.4-1.4)	7.8 (7.5-8)	5.7	6 (6-6)	4.8
Red-eyed Vireo	11	6	15th Feb-31st Mar	3.2 (2-4)	22 x 13.1	10-16	10-13	26	4.2 (0.8-12)	6.2 (2.9-13)	10.1 (4-38)	3.7 (0.3-8.0)	0.7 (0.1-3.3)	7.7 (6.5-10)	5.2 (4.5-5.5)	5 (4-6)	3.1 (3-3.4)
Plumbeous-backed Thrush*	0	5	27th Feb-19th Mar	3.8 (3-4)	27.7 x 20.9	9-14	9-14	17	3.8 (3-5)	6.8 (6-8)	11.8 (9-16)	0.7 (0.2-1)	0.8 (0.08-1.2)	15.6	9.5	8.2	5.8
Streaked Saltator	11	11	14th Feb-23rd Mar	2.5 (2-4)	19.7 x 17.5	11-14	12-13	27	2.8 (1.1-6)	5.2 (2.5-10)	8.1 (2-23)	1.8 (0.3-4.2)	0.7 (0.1-1.8)	14.1 (10-17.4)	9.8 (7.3-15)	7 (3-13)	5 (2-9)
Southern Yellow-grosbeak	27	16	9th Feb-25th Mar	2.8 (2-4)	27 x 19.5	10-13	8-15	32	4.3 (1.6-11)	5.8 (2.3-14)	12.3 (3-90)	2.4 (0.2-6)	1 (0.06-4)	11 (9-14)	8.2 (7.4-8.5)	4.5 (2.5-6.5)	2.5 (1.5-4.1)
Parrot-billed Seedeater*	1	0	21st Mar	2	NI	9+	11	20	2	3.5	3	1.2	0.8	6	5.5	4	3.2
Crimson-breasted Finch*	201	19	11th Feb-30th Mar	3 (1-4)	18.3 x 13.6	9-15	8-13	31	2.6 (0.5-5)	4 (0.8-7)	5.6 (0.5-13)	2.1 (0.03-6.5)	0.7 (0.05-4)	7.8 (6.7-9.3)	5 (4-5.5)	5.2 (3.2-7)	3.5 (2.5-4.8)
Collared Warbling-finch*	8	0	14th Feb-25th Mar	3 (1-4)	18.33 x 14.92	10-13	9-13	21	2 (0.5-3.5)	3.6 (1-5)	4.2 (3-7)	1 (0.08-2.5)	0.5 (0.1-1.3)	6.5 (5-8)	5.1 (5-5.2)	5.4 (4.5-6.3)	3.9 (3.5-4.3)
White-edged Oriole*	0	2	12th Feb-17th Mar	2.5 (2-3)	24.7 x 17.8	NI	NI	8	3.5 (3-4)	6.5 (5-8)	11.5 (3-20)	1.4 (0.5-2.2)	0.8 (0.3-1.2)	9.8 (9.5-10)	6.7 (6.3-7)	10.3 (9-11.5)	8.6 (7-10.2)
Scrub Blackbird*	0	7	4th-26th Feb	2.8 (2-3)	NI	~9	12	23	3.7 (3-5)	5.3 (5-6)	10.7 (6-16)	1.5 (0.4-3)	0.7 (0.3-1.2)	14.3 (13.5-15.3)	9.3 (8.5-10)	8.4 (7-10.3)	5.1 (4.2-6)

Figure 1. Inside the nest of the Necklaced Spinetail (*Synallaxis stictothorax stictothorax*), with three eggs visible.

Figure 2. Nest from above (top left) and side (top right), view of recently hatched chick and egg

through nest hole (bottom left) and egg (bottom right) of the Elegant Crescentchest (*Melanopareia elegans*).

Figure 3. Egg of the Fasciated Wren (*Campylorhynchus fasciatus*).

Figure 4. Nest (left) and egg (right) of the Speckle–breasted Wren (*Thryothorus sclateri*).

Figure 5. Nest (left) and egg (right) of the Plumbeous–backed Thrush (*Turdus reevei*).

Figure 6. Egg of the White–edged Oriole (*Icterus graceannae*).

Chapter 6 - Mixed species flocking in relation to food and predator abundance in the Tumbesian region of Ecuador

Introduction

Foraging in mixed species groups is common in many taxa, including birds, fish and primates (Morse 1970, Dolby and Grubb 2000). The potential of these groups to be models for community ecology has recently been recognized, and, given their global ubiquity, they offer opportunities for examining patterns across different communities (Goodale et al. 2010). Theory predicts that the benefits of mixed species foraging must outweigh the costs for the majority of individuals that participate. However, little is known about the cues individuals use to decide to participate in a mixed species group. Further, little is known about how the benefits of mixed group participation differ for individuals with different roles and across landscapes with differing predator and resource abundances. Birds represent one group where foraging in mixed groups (mixed species flocks) is pervasive, especially in tropical regions where flocking occurs year-round and includes a large proportion of the bird community—suggesting that flocking has a great positive effect on the fitness of individuals of these species (Hutto 1987, Chen and Hsieh 2002, Maldonado-Coelho and Marini 2004, Pomara et al. 2007). Here, I evaluate the proposed explanations for why birds participate in mixed species flocks in a highly threatened coastal tropical dry forest with high avian endemism in Ecuador. I also examine how a species' role in a mixed flock influences the benefits they incur. This study is unique in that I examine both the predator abundance and prey base availability for insectivorous birds across a human altered landscape, and examine differences in the benefits of flocking to both sit-and-wait solitary and intraspecifically gregarious nuclear species, as well as follower species.

Birds are thought to have evolved to participate in mixed flocks to gain fitness via either: 1) enhanced protection from predatory raptors due to earlier warning calls or lower probability of being singled out; or 2) greater foraging efficiency due to the flushing of arthropods as the flock moves through an area, kleptoparasatism (i.e., stealing food from other flock members), learning new methods of food capture from other flock participants; or some combination of factors (Moynihan 1962, Powell 1985). Moreover, flock members may enjoy both reduced predation risk and increased foraging efficiency if they are able to spend less time scanning for predators when in flocks than foraging singly or in pairs (Sullivan 1984, Elgar 1989, King and Rappole 2000). The relative importance of predator avoidance and feeding benefits as drivers of mixed flocking behavior is still debated and appears to differ depending on the region studied—although a recent analysis of flocks from around the world pointed to avoidance of predation as the most important factor in flock evolution (Sridhar et al. 2009). While theories advanced to explain mixed species foraging flocks focus on benefits to individuals for participating, birds may also suffer costs. These possible costs include competition for food resources, kleptoparasatism by other flock members, the necessity to modify foraging locations or methods, and increased conspicuousness to predators due to the larger group size (Hutto 1988, Terborgh 1990). However, in a comprehensive study of the survival rates of birds in three categories (obligate, facultative, and non-flockers) in various humid forests, Jullien and Clobert (2000) found that species that regularly participate in mixed flocks do show higher survival rates than species that rarely or never participate. Despite this, tropical birds vary considerably in the amount of time they spend foraging with a mixed flock (termed flocking propensity); ranging from never participating, to occasionally participating, to always participating. Differences in food and predator abundances, vegetation structure, flock-mates and species-specific traits (such as feeding technique or dominance level) might account for variation in the relative costs and benefits of flock participation for a particular species or individual and may help to explain these inter and intraspecific differences in flocking propensities (Terborgh 1990, Thiollay 1999).

Machalilla National Park, in the Tumbesian region of coastal Ecuador, provides an ideal landscape in which to study mixed flocking behavior for the following reasons: 1) very little is known about the birds of the region, but a prior study indicated that mixed flocks in this region are unique in several ways from mixed flocks in other tropical areas, suggesting they warrant further study (Ch. 3); 2) the park encompasses both coastal arid scrub and tropical dry forest vegetation in a gradient of intensity of human use, allowing for examination of how birds' flocking propensities and possible factors influencing these propensities vary in different areas of the landscape; and 3) earlier work showed that species' flocking propensities do vary by vegetation type in the park (Ch. 3). In a previous study I showed that mixed species flocking is clearly an important part of the biology of birds in the Tumbesian region, as the majority of species in Machalilla National Park did participate to some degree in mixed flocks during the breeding season (Ch. 3). Further, I found that the mixed flocks had much higher average numbers of individuals than have been previously reported in most areas of the Neotropics (Ch. 3). I determined that forest disturbance from rural community activities has a negative effect on average flock sizes and birds' flocking propensities in Machalilla National Park (Ch. 3). However, I did not examine the causal mechanisms responsible for these observed differences in flocking propensities. For instance, the abundances of both arthropods and forest raptors have been shown to decline with increasing habitat disturbance (Thiollay 1999, Tovar-Sanchez et al. 2004, Barbaro et al. 2005, Rango 2005), which might in turn influence species' propensities to flock. Raptors are the only predator of birds foraging in flocks during the day, and all flocking species are primarily insectivorous. My objective here was to test hypotheses about the cues for mixed flocking for specific species in the Tumbesian region by relating local food and predator abundances to species' flocking propensities and feeding rates in and out of mixed flocks (Powell 1985, Hutto 1994, Latta and Wunderle 1996, King and Rappole 2000).

Based on results from other studies (Jullien and Thiollay 1996, Thiollay 1996, 1998, Tovar-Sanchez et al. 2004, Buler et al. 2007), I predicted that more disturbed areas of Machalilla National Park would have both lower arthropod prey abundances and lower predatory raptor abundances, which would allow me to separate two cues related to each of the proposed primary benefits of joining mixed species flocks. If species are participating in mixed flocks primarily because the gain in feeding benefits is greater than the costs of participation, I expected the following: 1) birds would show greater foraging efficiencies while with a mixed flock than when alone or with conspecifics; 2) the cue for flocking would be low arthropod prey abundance; and 3) species would show the highest flocking propensities in the areas with the lowest arthropod prey abundances, which I predicted would be in more disturbed vegetation. However, if species are participating in flocks primarily because the benefit of predation avoidance is greater than the costs of participation, I expected the following: 1) the cue for flocking would be high predatory raptor abundance; and 2) species would show the highest flocking propensities in areas with the greatest predatory raptor abundances, which I predicted would be in less disturbed vegetation. I hypothesized that in the Tumbesian region, predator avoidance would better explain flocking behavior than a gain in feeding benefits.

The fact that different species show different propensities to flock, both generally (Thiollay 1999, Pomara et al. 2007) and in Machalilla National Park (Ch. 3), suggests that species-specific traits such as feeding technique or dominance level are also important determinants of the benefits or costs of mixed flock participation (Terborgh 1990, Thiollay 1999). For example, nuclear species, which are thought to be important in the formation and maintenance of cohesion of mixed flocks, may not benefit from being in a flock to the same degree as follower (also called satellite) species, or may not benefit at all (Moynihan 1962, Hutto 1994, Hino 1998, Goodale and Beauchamp 2010). This is because nuclear species are often more highly vigilant for predators than other flock members, for one of the following reasons: 1) they are sit-and-wait foragers and thus have more time to scan for predators than other more active flock members; 2) they are species that travel in large family groups and have thus likely already developed an early-warning system for their kin (Powell 1985, Munn 1986, Terborgh 1990, Jullien and Clobert 2000, Sridhar et al. 2009). Therefore, I also predicted that the benefits gained by species while in mixed flocks would vary based on the role of the species in the flock. Despite the recent increase in interest in determinants of mixed flocking behavior, few studies to date have examined how these determinants differ at landscape scales depending on predator and prey abundances and species' roles in the flock.

Methods

Study site

The Tumbesian region of south-western Ecuador and north-western Peru encompasses the great majority of remaining coastal tropical dry forest in South America, and is one of the most threatened bioregions in the world due to heavy human use in the form of development and livestock grazing (Best and Kessler 1995). The region is among the five most species rich regions of the world in terms of avian endemic species, and is home to 32 threatened or near threatened birds and 61 endemic bird species (Wege and Long 1995). Machalilla National Park, on the southwestern coast of Ecuador, is one of the largest parks in this region (55,095 ha), containing 67% of its endemic bird species (Wege and Long 1995). Despite its status, many areas within the park suffer from continual degradation from human use, and the rest of the vegetation is in some stage of recovery from excessive grazing and removal of trees for charcoal production (Zambrano and Vargas 1998). Several small communities still exist within the park and residents make a living by farming goats, cattle, horses and pigs—all of which roam freely in the park and cause considerable damage to the vegetation (pers. obs).

The park has a marked gradient of rainfall caused by differences in elevation (0 to 860 m) and slope position relative to the coast. As a consequence, the vegetation gradient ranges from arid scrub at the lowest elevations nearest to the ocean to tropical dry forest further inland to humid and fog forest up in the hills, and generally represents the vegetation types found more broadly across the entire Tumbesian region. I studied mixed species flocks in two common vegetation types within the park—arid scrub and tropical dry forest—under two disturbance levels each (low and moderate), for a total of four different vegetation/disturbance combinations. I verified these *a priori* habitat and disturbance classifications by recording the abundances of domestic animals (pigs, horses, goats and cattle) each month along the same transects used for bird counts (see below) and evaluating forest structure and composition in a series of vegetation plots (I Ch. 1). Arid scrub consists primarily of low, bushy trees and cacti and has an average canopy height of 4.84 (±0.25) meters. Prominent plant species in arid scrub include *Caesalpinia corimbosa*, *Cordia lutea* and *Armatocereus cartwightianus*. Tropical dry forest is similar to arid scrub, but differs by having trees with diameters more than twice that of the biggest trees in arid scrub, an average canopy height of 8.19 (±0.50) meters, and greater canopy density. Trees that are common in tropical dry forest include *Ceiba trichistandra*, *Zizyphus thyrsiflora* and *Mutingia* *calabura*. Low disturbance sites were in a part of the National park that has been protected from most rural community activities for over 30 years. Moderate disturbance sites were next to rural communities where people often harvest trees and shrubs for charcoal production and house building and allow their domestic animals to roam freely.

Flocking propensities and foraging rates

I defined a mixed species foraging flock as more than one species traveling at a maximum of 10 m from any other species in the flock for at least 10 minutes (we counted birds in pairs or family groups as solitary (Moynihan 1962, Hutto 1994)). Mixed species foraging flocks of birds occur in all of the vegetation types in the park, with participants including 25 of the region's endemic species, four of which are listed as endangered or vulnerable (IUCN 2010). Flocks remained active throughout the day, with no apparent resting period (pers. obs). To determine flocking propensities of as many species as possible I systematically walked 2 km on existing paths within each vegetation type from one hour after sunrise to one hour before sunset once a month from February to May 2008 and 2009. I was careful to uniformly cover each site so that the same individuals were not encountered repeatedly, and each bird I observed I noted as being in a flock or solitary. Flocking propensities were calculated by combining observations from all flocking propensity surveys in a vegetation type and dividing the number of flocking individuals of a species by their total detections during the flocking propensity walks (Pomara et al. 2007, Chapter 1). Birds' flocking propensities were significantly greater in less disturbed compared to more disturbed tropical dry forest, but did not differ across the disturbance gradient in arid scrub (n = 55 species; reported in Ch. 1).

I determined species' foraging rates by recording the time in seconds between two food captures for individuals where it was possible to see four consecutive captures. The sample size was 30 individuals of each focal species in each vegetation type, for a total of 90 time intervals per species per vegetation type. Focal species for which I could gather a large enough sample size on feeding rates in and out of flocks included the endemic crimson-breasted finch (*Rhodospingus cruentus*), collared antshrike (*Sakesphorus bernardi*), and necklaced spinetail (*Synallaxis stictothorax*); and the non-endemic red-eyed vireo (*Vireo olivaceus*), southern beardless-tyrannulet (*Camptostoma obsoletum*), tropical gnatcatcher (*Polioptila plumbea*), and tawny-crowned pygmy-tyrant (*Euscarthmus meloryphus*) (see Ch. 1). I identified nuclear species in flocks in all vegetation type/disturbance combinations by their large intraspecific group sizes, high flocking propensities, regularity of occurrence in flocks, conspicuous calls or behavior, and leadership role in the flocks (Moynihan 1962, Hutto 1994, Goodale and Beauchamp 2010). All focal species but the crimson-breasted finch, southern beardless-tyrannulet and tawny-crowned pygmy-tyrant are nuclear flocking species (reported in Ch. 1), and of those all but the collared Antshrike are intraspecifically gregarious (i.e., travel and forage throughout the day with more than one conspecific). All bird observations were done on days without rain or strong wind.

Arthropod and predator abundances

The great majority of species participating in mixed species flocks are primarily insectivores. While determining the availability of insects and spiders as a food resource to birds is very difficult, relative differences in arthropod abundance among vegetation types has been reliably estimated (Cooper and Whitmore 1990, Wolda 1990, Poulin et al. 1992). I used three sampling methods—malaise traps, pitfall traps, and sweep-netting—to try to cover all strata in which the birds forage. Malaise traps target flying arthropods, pitfall traps target ground-dwelling arthropods, and sweep-netting targets arthropods living on vegetation. Arthropods captured with all three methods were killed by immersion in 70% isopropyl alcohol. I placed five malaise and pitfall traps 200 m apart in each vegetation type and left the traps open from dawn till dusk for two consecutive days. Each vegetation type and disturbance level was censused twice per month from February to May of 2009. After each sampling period trap contents were separated into individual arthropods which were identified to order, measured (length and width of the widest parts) and weighed to the nearest 0.01 g either individually for larger specimens or as a group for smaller specimens using a digital electronic scale. Sweep-netting was conducted on a total of 10 trees and shrubs per vegetation type, with care taken to cover a representative sample of the local vegetation. Each vegetation type and disturbance level was sampled once per month and captured arthropods were indentified, measured and weighed as above. Although no food-resource sampling method can be perfect, these methods combined provide a general proxy of differences in arthropod abundance and therefore food availability among sites. While some arthropods captured were likely more desirable prey items than others due to their higher nutritional value (e.g., Orthopterans and Lepidoptera larvae), I am confident that the great majority of trap and sweep-net captures were from groups eaten by flock participants (see Table 1 for abundances of each order captured). For example, in a recent large-scale analysis of the diets of over 1000 individuals of more than 50 Brazilian understory forest birds, the principal groups of invertebrates consumed were Formicidae, Isoptera, Coleoptera, Araneae and non-Formicidae Hymenoptera (Manhaes et al. 2010). Other studies have found that Orthopterans and spiders are also common prey for tropical forest understory birds (Gradwohl and Greenberg 1982, Rosenberg 1990). These orders were also the most commonly captured in the traps and sweep-nets.

Raptors are the main diurnal predator of small birds. I censused raptors in each vegetation type and disturbance level for a total of four hours twice a month from Feb to May of 2009, and recorded the species and number of individuals observed. This time included two hours in the late morning (10-12 am) watching for soaring or perched raptors from a high vantage point overlooking the forest, and two hours later in the day (12-2 pm) searching each vegetation type on foot for perched or low-flying raptors (sensu Thiollay 1999).

Statistical analyses

To test for differences in feeding rates of species in and out of flocks in different vegetation types, I log-transformed feeding rates and then used a two-way analysis of variance with Tukey HSD post-hoc tests. Due to low sample sizes I pooled the weights of all arthropods (insects and spiders) caught in all trap types across the four month sampling period in each vegetation type and disturbance level. I then log-transformed the biomass totals and used a one-way ANOVA followed by Tukey HSD multiple comparisons on each to test for differences in prey biomass between the vegetation types and disturbance levels. Similarly, I grouped all potential predator (raptor) individuals of all species seen in hilltop and trail surveys in each vegetation type across the four-month sampling periods. I then log-transformed the counts of individuals, but a Shapiro-Wilk’s W test still showed the data were significantly different from normal. I therefore used a Kruskal-Wallis test with Mann-Whitney U tests for pairwise comparisons to compare predator abundances between vegetation types. All analyses were run using SPSS 18 (2010).

Results

Feeding rate differences

The feeding rates of tropical gnatcatchers, necklaced spinetails and red-eyed vireos did not differ in and out of flocks across all vegetation types and disturbance levels pooled or within any vegetation type or disturbance level (Table 2, Fig. 1a, b, c). However, when feeding rates both in and out of flocks were pooled these species showed significantly higher feeding rates in less disturbed compared to more disturbed areas. Data on tawny-crowned pygmy-tyrants and crimson-breasted finches were only recorded across the disturbance gradient in arid scrub, and both species showed significantly greater feeding rates in flocks than out of flocks and in less disturbed compared to more disturbed areas (Table 2, Fig. 1d, e). Southern beardless-tyrannulets and collared antshrikes had significantly higher feeding rates in flocks than out of flocks across all vegetation types and disturbance levels pooled and within all vegetation types and disturbance levels (Table 2, Fig. 1f, g). Further, when all feeding rates both in and out of flocks were pooled these species showed significantly higher feeding rates in less disturbed compared to more disturbed areas and in less disturbed tropical dry forest compared to less disturbed arid scrub.

Arthropod and predator abundance differences

Arthropods from at least 20 different orders were caught in the three trap types, with the greatest numbers of individuals belonging to hymenoptera, coleoptera and arachnida (Table 3). Most individual arthropods were caught in pit fall traps (6032), then with sweep-netting (2992), and the fewest in malaise traps (2717). A total of 2429 individuals were caught in less disturbed arid scrub, 4733 in more disturbed arid scrub, 2293 in less disturbed tropical dry forest, and 2400 in more disturbed tropical dry forest. However, arthropod biomass did not differ significantly across any of the vegetation types or disturbance levels ($F = 2.213$, $df = 3$, $p = 0.89$), although confidence intervals all crossed zero, suggesting there may not be enough power to detect differences. Eight species of raptors that small birds may perceive as predators were identified in the surveys: bat falcon (*Falco rufigularis*), crane hawk (*Geranospiza caerulescens*), hook-billed kite (*Chondrohierax uncinatus*), laughing falcon (*Herpetotheres cachinnans*), harris's hawk (*Parabuteo unicinctus*), great black hawk (*Buteogallus urubitinga*), southern crested caracara (*Caracara plancus*), and peregrine falcon (*Falco peregrines*). Predatory raptor abundances were different across the vegetation types and disturbance levels ($X^2 = 23.822$, $df = 3$, $p < 0.000$), but multiple comparisons showed that this was the case only in that less disturbed tropical dry forest had higher raptor abundances than all other vegetation types; no other comparison was significant (i.e., less disturbed compared to more disturbed tropical dry forest $U = 33.5$, $p < 0.001$, arid scrub less disturbed compared to arid scrub more disturbed $U = 113$, $p = 0.557$, less disturbed tropical dry forest compared to less disturbed arid scrub $U = 20.50$, $p < 0.001$, less disturbed arid scrub compared to more disturbed tropical dry forest $U = 114.00$, $p = 0.586$, more disturbed arid scrub compared to more disturbed tropical dry forest $U = 127.50$, $p = 0.984$, more disturbed arid scrub compared to less disturbed tropical dry forest $U = 22.5$, $p < 0.001$).

Discussion

My prediction that in the Tumbesian region birds are forming mixed flocks primarily to avoid predation rather than to accrue feeding efficiency benefits was supported, in that high raptor abundance seemed to be greater cue for birds to join mixed species flocks than low arthropod prey abundance. However, mixed flock participants were also able to forage at higher rates when in flocks than when alone or with conspecifics, suggesting that birds gain feeding benefits as a side effect of choosing to be with mixed species flocks to avoid predation. More specifically, I found that predatory raptor abundance was significantly greater in less disturbed tropical dry forest where birds' flocking propensities are greatest, but did not change across the disturbance gradient in arid scrub. Further, I found that arthropod prey biomass did not change significantly across the vegetation or disturbance gradient in either arid scrub or tropical dry forest, but that this was likely due to low sample sizes. Arthropod biomass was greater in less disturbed than more disturbed vegetation, especially in tropical dry forest where birds' flocking propensities are the highest. Support for both the foraging and antipredator hypotheses of mixed species flocking has been found elsewhere, via a decrease in individual vigilance levels in flocks allowing more time for prey capture (e.g., Chen and Hsieh 2002, Hart and Freed 2005). Conversely, in other regions one or the other hypothesis was supported but not both (e.g., Poulsen 1996b, Jullien and Thiollay 1998, King and Rappole 2001).

Predatory raptor and arthropod prey biomass

Both predatory raptor abundance and flocking propensities of birds were higher in less disturbed compared to more disturbed tropical dry forest but did not differ across the disturbance gradient in arid scrub. This suggests that in tropical dry forest predator avoidance may be an important impetus for joining flocks. If species perceive that the benefits of being in a flock are fewer in more disturbed areas because of a lower risk of predation, they are likely to show lower flocking propensities in those areas. However, previous work showed that species' feeding efficiencies in mixed flocks were lower in the smaller flocks in more disturbed areas than in the larger flocks in less disturbed areas (Ch. 3), suggesting that these species do suffer costs from other individuals lowering their flocking propensities in more disturbed sites. There was no statistically significant difference in arthropod prey biomass across the vegetation types or disturbance gradients but greater biomass in less disturbed areas, suggesting that the lowered feeding efficiencies of birds in mixed flocks in more disturbed areas compared to birds in flocks in less disturbed areas results either from lower prey biomass or from costs of being with a smaller mixed flock. These costs may stem either from a lack of other species from which to learn new methods of food capture or steal food, or because prey is not flushed as readily from the vegetation (Moynihan 1962, Powell 1985). Regardless of the reason for the observed lower feeding efficiencies in more disturbed areas, the fact that the birds are not compensating for this cost by increasing their flocking propensities suggests that they use perceived predation threat as a cue for flock formation rather than foraging efficiency. If this is true, then an increase in foraging efficiency gained from being in a flock is simply an added benefit to the reduction in predation risk, and may not have been as important for the evolution of flocking behavior.

It is also possible that I did not find a relationship between food abundance and flocking propensities because I only collected data for part of the year, during the rainy season. For example, several studies of flocks in tropical forests found increased rates of flocking during periods of low insect availability, suggesting that individuals were flocking at least in part to increase their food intake (Poulsen 1996a). However, birds also tend to participate less in flocks during the breading season, which coincides with the period of highest insect abundance (Develey and Peres 2000). Given these two patterns, separating the effect of the birds' breeding season on flock participation from the effect of prey availability can be difficult. Here, I mitigated this problem by examining the relationships of birds' flocking propensities to prey abundance for only four months during the wet season (birds' breeding season), when arthropod abundance should be more constant than if I were comparing the wet and dry seasons.

Feeding rates

While it has been suggested that many flock participants may be suffering costs rather than accruing benefits with regard to food acquisition in large mixed species flocks (Rabenold and Christensen 1979, Hino 1998), in this study the majority of focal species did capture prey at a higher rate when they were with a flock compared to foraging on their own or with conspecifics; a result found elsewhere for different species (Thiollay 1988, Develey and Peres 2000, Sridhar et al. 2009). My prediction that species would show greater foraging efficiencies while in a mixed flock than out was supported for all species examined except those that are intraspecifically gregarious nuclear species. The intraspecifically gregarious nuclear species did not gain a feeding benefit by being in flocks in any vegetation type/disturbance level combination, while the one nuclear species that was not intraspecifically gregarious (collared antshrike) did, as did the non-nuclear (satellite) species. This result was also documented in a tropical forest in Madagascar, where the intraspecifically gregarious nuclear species did not gain a feeding benefit from foraging with mixed specific flocks while the non-intraspecifically gregarious nuclear species did (Hino 1998). Intraspecifically gregarious species are more likely to have evolved an early warning system for predator detection (Hamilton 1964, Maynard Smith 1965), and thus these species are thought to participate in mixed species flocks more to increase foraging efficiency than to decrease predation risk or are joined by other species rather than choosing to be in mixed flocks (Hino 1998, Chen and Hsieh 2002). The fact that the intraspecifically gregarious species did not gain a feeding benefit in this region, however, suggests that these species may be joined by other species and are not actively seeking out mixed flock participation. Non-nuclear species might follow these intraspecifically gregarious species to take advantage of both foraging (via flushing of prey, reduced time needed for vigilance, exploitation of new, more vulnerable niches) and predator protection (via alarm calls) benefits (Chen and Hsieh 2002); suggesting that this interaction yields a positive benefit to the followers of intraspecifically gregarious species and has a neutral effect on the intraspecifically gregarious species. However, Hino (1988) pointed out that a reduced risk of predation for flock members is likely a necessary consequence of flocking while a gain in feeding efficiency is not, meaning that the intraspecifically gregarious species may experience some antipredator benefits by being in a mixed flock due to the larger group size or by responding to other species' alarm calls (e.g., Goodale and Beauchamp, 2010). Using meta-analyses of published results on flocks from around the world, Sridhar and colleagues (2009) found that flock followers but not nuclear species increase their foraging rates and reduce their vigilance compared to when they are foraging solitarily or in conspecific groups. This suggests that species often follow nuclear species whose vigilance they can exploit, thereby both reducing their risk of predation and foraging at a higher rate (Sridhar et al. 2009). However, these analyses did not separate intraspecifically gregarious and solitary nuclear species, which here turned out to be an important distinction.

Foraging methods

Several authors have reported that actively foraging species (those that are constantly moving to glean or probe for prey) join flocks more frequently than less active foragers (those that sit and wait until they see prey) because of their greater visibility to predators (Thiollay and Jullien 1998, Sridhar et al. 2009). In Machalilla National Park, however, the majority of birds employ an active foraging mode—making determining whether they were overrepresented in flocks difficult. Of the 39 species that participated in flocks more than half the time, 28 were active foragers. Sridhar and colleagues (2009) suggest that flocks might consist of a mix of active foragers that gain antipredator benefits and sit-and-wait foragers that gain foraging benefits. In this study, some of the most active foragers were also the intraspecifically gregarious nuclear species, but they did not gain feeding benefits from being in mixed flocks while some of the focal sit-and-wait species did.

In some areas birds were documented to change their foraging techniques, heights and locations to more closely match those of other species when they were in mixed species flocks, supporting the hypothesis of species' gaining feeding benefits from flocking by copying feeding strategies of other species (Hino 1998). Conversely, in other areas birds in mixed species flocks showed little to no overlap in foraging techniques or locations (King and Rappole 2001). Here, I did not explicitly examine differences in species' foraging methods or locations; however, based on many hours of flock observations I noted that participants did appear to show great overlap in foraging locations and techniques. For example, the elegant crescentchest (*Melanopareia elegans*) and collared warbling-finch (*Poospiza hispaniolensis*) have roughly equal body masses (14.5 and 13.5 cm) and foraged almost exclusively on the ground. The necklaced spinetail (*S. stictothorax*), tropical gnatcatcher (*P. plumbea*) and red-eyed vireo (*V. olivaceus*) also are similar in body size (12.5, 11 and 14.5 cm) and foraged in low to mid levels using similar gleaning and sallying techniques (all are intraspecifically gregarious). The southern-beardless tyrannulet (*C. obsoletum*) and pacific elaenia (*Myiopagis subplacens*) (10 and 14 cm) both sallied for prey at mid-level heights, while the southern yellow grosbeak (*Pheucticus chrysogaster*) and streaked saltator (*Saltator striatipectus*) are very close in body size (21 and 20 cm) and foraged in mid to high levels. Future studies in the region should examine more explicitly how these feeding techniques and locations overlap and how they change when a species is foraging with a flock versus alone or with conspecifics.

Limitations and Perspectives

Mixed species flock participants often differ with regard to the costs and benefits they accrue from flocking, depending on their social position in the flock, foraging technique and the vegetation type in which they are flocking (e.g., Hutto 1988, Hino 1998, 2000). In Machalilla National Park birds appeared to be joining flocks primarily to avoid predation, and all focal species but those that were intraspecifically gregarious nuclear species (i.e., necklaced spinetail, tropical gnatcatcher, red-eyed vireo) foraged at a higher rate while in a flock versus when solitary or with conspecifics. This study had several limitations, including a low sample size of species whose feeding rate both in and out of flocks I was able to determine, a low sample size of arthropod biomass across the vegetation types and disturbance gradients, and that I did not take into account phylogenetic relationships among species. Phylogenetic relationships among species can be important because a large component of character variation (for example, flocking behavior) among species that co-occur in the same ecological community may be associated with phylogeny and is therefore not independent (Freckleton et al. 2002). However, phylogenetic relationships were not available for the species in this study. Moreover, while predation pressure or food shortages may be important drivers of flocking behavior, other factors such as those determining home range sizes may also contribute (e.g., Pomara et al. 2007). However, this study is unique in that I was able to examine both the predator abundance and prey base availability for insectivorous birds across a human-altered landscape. In addition, I examined differences in the benefits of flocking to both sit-and-wait solitary and intraspecifically gregarious nuclear species, as well as follower species. Future work can build on the results presented here by examining how movement rates, foraging strategies and positions vary for species in and out of flocks and by including a larger sample of flocking species found within the Tumbesian region and more complete data on arthropod biomass. Moreover, testing similar hypotheses to the ones tested here, such as whether species form mixed groups to avoid predation or gain feeding benefits and whether all participating species benefit from being in a mixed group to the same degree, remains to be done with other taxa and could yield a greater understanding into community ecology and the evolution of mixed species grouping (Sridhar et al. 2009, Goodale et al. 2010).

Table 1. Two-way ANOVA results for the feeding rate differences of each of seven species in each vegetation type (arid scrub and tropical dry forest) and disturbance level (less disturbed and more disturbed), in and out of flocks, and in and out of flocks within each vegetation type and disturbance level in 2008 and 2009 in Machalilla National Park, Ecuador (n = 30 individuals and 90 time intervals for each species in each category; df = 1).

Species	**Effect**	**F**	***p***
Collared Antshrike	Veg type	101.472	<0.001
	In/out of flock	61.293	<0.001
	Veg type x In/out of flock	3.570	0.014
Crimson-breasted Finch	Veg type	60.286	<0.001
	In/out of flock	70.766	<0.001
	Veg type x In/out of flock	10.407	0.001
Necklaced Spinetail	Veg type	98.845	<0.001
	In/out of flock	0.433	0.511
	Veg type x In/out of flock	1.801	0.145
Red-eyed Vireo	Veg type	60.643	<0.001
	In/out of flock	0.860	0.354
	Veg type x In/out of flock	1.425	0.234
Southern Beardless-tyrannulet	Veg type	53.719	<0.001
	In/out of flock	82.491	<0.001
	Veg type x In/out of flock	0.413	0.001
Tropical Gnatcatcher	Veg type	87.787	<0.001
	In/out of flock	1.424	0.233
	Veg type x In/out of flock	2.010	0.111
Tawny-crowned Pygmy-tyrant	Veg type	142.199	<0.001
	In/out of flock	461.337	<0.001
	Veg type x In/out of flock	0.478	0.012

Table 2. Total biomass of arthropods collected in all trap types and total numbers of individuals of predatory raptors observed in each vegetation type (arid scrub and tropical dry forest) and disturbance level (LD = less disturbed, MD = more disturbed) in 2009 in Machalilla National Park, Ecuador.

Vegetation type/ disturbance level	**Arthropod biomass (g)**			**Predator abundance**		
	Total	**Mean/ transect**	**SD**	**Total**	**Mean/ transect**	**SD**
Arid scrub, LD	63.110	1.753	1.995	23	1.438	0.964
Arid scrub, MD	51.180	1.422	1.440	20	1.250	1.125
Tropical dry forest, LD	121.160	3.366	4.379	73	4.563	2.449
Tropical dry forest, MD	55.440	1.540	1.622	23	1.438	1.672

Table 3. Total numbers of individuals of each arthropod order captured in all trap types combined in each vegetation type (arid scrub and tropical dry forest) and disturbance level (LD = less disturbed, MD = more disturbed) in 2009 in Machalilla National Park, Ecuador.

Order	Tropical dry forest, LD	Tropical dry forest, MD	Arid scrub, LD	Arid Scrub, MD
Arachnida	172	189	283	345
Chilopoda	1	0	0	0
Coleoptera	486	1136	438	524
Dermaptera	4	15	0	3
Dictyoptera	25	26	8	19
Diplopoda	1	0	0	1
Diptera	58	58	107	36
Hemiptera	76	51	71	59
Hymenoptera	790	2620	442	562
Inch worm	76	25	115	78
Isopoda	44	6	171	108
Isoptera	0	0	0	2
Lepidoptera	29	18	26	20
Mantodea	2	1	1	1
Neuroptera	4	4	0	0
Odonata	0	0	3	0
Orthoptera	138	114	96	89
Phasmida	0	0	8	6
Scorpiones	4	2	16	15
Siphonaptera	2	4	0	0
Thysanura	14	25	0	6
Very small[1]	503	439	508	526

[1] Very small arthropods were not identified to order.

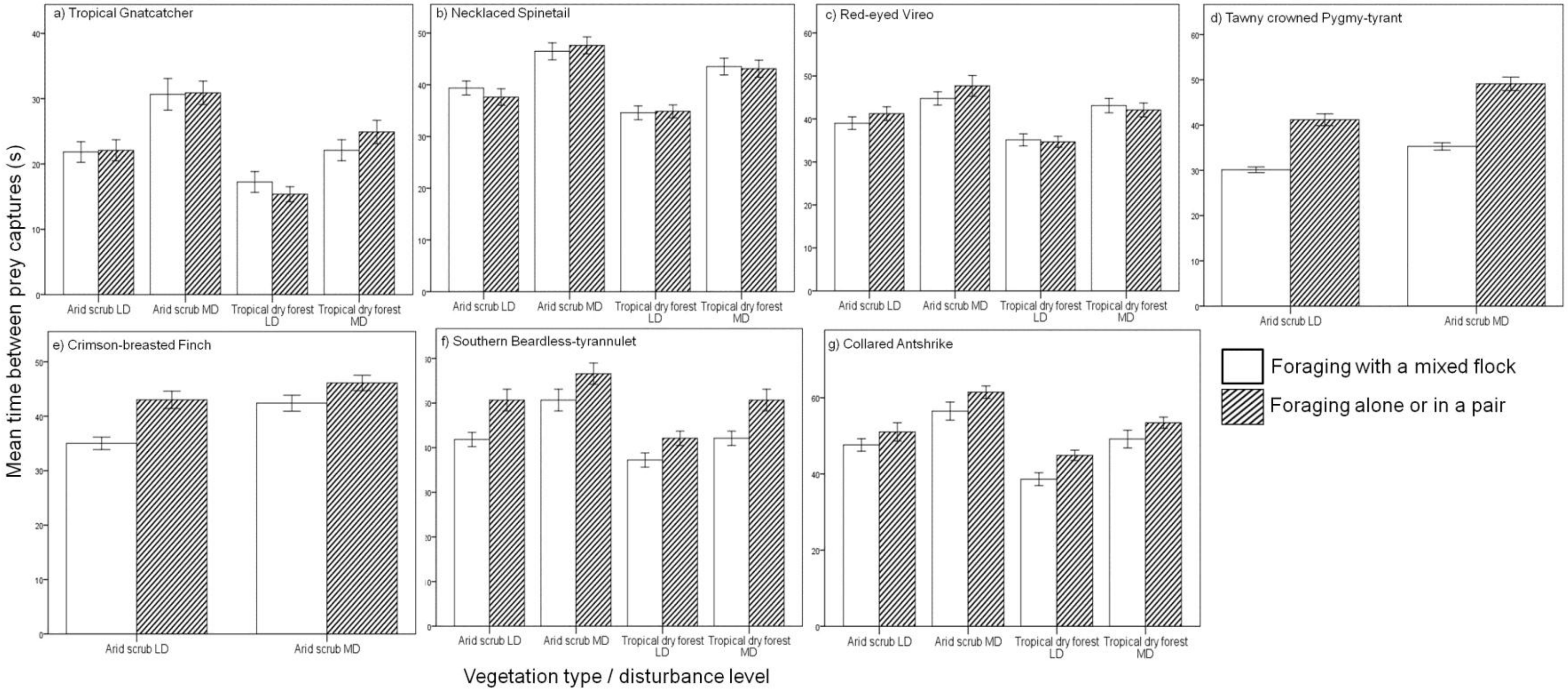

Figure 1. Mean time between two prey captures for each of seven species in each vegetation type (tropical dry forest and arid scrub) and disturbance level (LD = less disturbed, MD = more disturbed) separated by whether the birds were observed with a flock (plain bars) or solitary (diagonally lined bars; n = 30 individuals and 90 time intervals for each species in each category).

Chapter 7 – Conclusions

Through the completion of my dissertation I was able to determine that mixed species flocks of birds in the Tumbesian region display some unique characteristics from flocks in the temperate zone and other tropical regions; that species' responses to habitat degradation are often dependant on vegetation type, even within the same landscape; and that members of mixed species flocks in the Tumbesian region benefit both from increased feeding efficiency and lowered risk of predation, but that different species benefit in different ways.

In my review of the results of experiments in behavioral landscape ecology I found the following general trends: (1) movement was usually faster and more directional in unfamiliar or sub-optimal areas; (2) substantial detours were often taken through preferred habitat to avoid gaps in that habitat; (3) movement appeared to be augmented for most taxa when corridors were present in a given landscape; (4) movement patterns depended not only on the characteristics of the patch the animal was in, but also on those of the surrounding landscape as well; (5) movement behavior and homing ability differed between habitat generalists and specialists; and (6) translocated animals often exhibited different behavior than residents. As for habitat selection, the trade-off between food or other resource availability and predation risk was especially apparent; conspecific cues were important in habitat choice and the perception of predation risk altered feeding and other behaviors. Further, reproductive success was generally lower in edge vegetation, predation perception affected reproductive effort, and pairing success often decreased in disturbed vegetation. These results allow processes within the theoretical framework of behavioral landscape ecology to be quantified, which can also guide model parameterization when experimental validation is not possible.

In chapters 3 and 4, I examined the effect of habitat degradation due to two pervasive rural community activities (tree cutting and livestock grazing) on the bird community in the Tumbesian region of Ecuador. Small-scale livestock grazing may have minimal negative impacts and might provide a good example of how people can benefit from land use while at the same time conserving biological diversity. In Chapter 3, I found that in the Tumbesian region of Ecuador livestock grazing and other rural community activities had little impact on mixed species flocks of birds in arid scrub, but that there were large negative impacts in tropical dry forest vegetation. These results indicate that small scale grazing may not always be detrimental to native fauna, but that results from one area cannot be safely generalized to different vegetation types even within the same landscape. Further, I found that by examining other indicators in addition to species richness I gained a more complete picture of the impacts of these human disturbances. In this case, studying species' interactions and reproductive success allowed a greater negative impact from habitat degradation to be seen than if I had looked at species richness and abundance alone.

My results in Chapter 4 were consistent with my findings in Chapter 3, in that nest survival of most species appeared to be much more greatly negatively impacted by habitat disturbance in tropical dry forest than in arid scrub vegetation. For most groups of nests, day of the nesting season, vegetation type, year and nest type were important factors explaining variation in daily nest survival rates. In several groups the stage at which the nest was found was also important, but in only one group each was nest height, cover around the nest, and whether the nest was in a spiny plant or not important. The amount of weed and shrub cover within 5 m of the nest never showed up in the variables important in explaining variation in daily nest survival rates. These results suggest that in addition to seasonal variation on both short (daily) and long (yearly) time scales, factors at large spatial scales, such as vegetation type, are more important for nest survival than smaller scale location attributes such as weed and shrub cover or nest placement.

In Chapter 5, I presented descriptions of the nests, eggs, incubation and nestling periods and nest placement for 32 bird species, 14 of which are endemic to the Tumbesian region (Knowlton 2010). Egg or nest descriptions had not previously been published for seven of these species. Gaining information such as nest architecture and site, clutch size, and incubation and nestling periods not only allows for the examination of regional and local variation in these traits within species, but can be crucial to conservation efforts which aim to increase reproductive success of threatened species (Stauffer and Best 1986, Gill 1990).

Lastly, in Chapter 6, I determined that in the Tumbesian region birds are forming mixed flocks primarily to avoid predation rather than to accrue feeding efficiency benefits. However, participants were also able to forage at higher rates when in flocks than when alone or with conspecifics, suggesting that birds gain feeding benefits as a side effect of choosing to be with mixed species flocks to avoid predation. I found that the intraspecifically gregarious species (i.e., those that travel and forage during the day with more than one other conspecific) did not gain a feeding benefit from being in a mixed species flock. This suggests that in this region intraspecifically gregarious species may be joined by other species and are not themselves actively seeking out mixed flock participation. Other, more solitary species might follow these intraspecifically gregarious species to take advantage of both foraging (via flushing of prey, reduced time needed for vigilance, exploitation of new, more vulnerable niches) and predator protection (via alarm calls) benefits (Chen and Hsieh 2002).

My findings highlight the importance of examining multiple indicators when attempting to predict species' long term persistence or creating conservation management plans. For example, determining how species richness, abundances, interactions, behavior and reproductive success varied across a landscape consisting of various levels of human disturbance allowed me to gain a more complete picture of species specific and community wide impacts of disturbance on birds in this region. Based on my findings, I predict that implementing the following would most likely increase the conservation potential of the Tumbesian region: 1) increase restrictions on livestock grazing and the numbers of houses allowed in existing protected areas in Ecuador and Peru that contain tropical dry forest, 2) designate new protected areas to encompass tropical dry forest that is currently not protected, 3) use predictive models to estimate how tropical dry forest will move with climate change to increase protection of those areas as well, and 4) increase local community awareness of the sensitivity of tropical dry forest to degradation and offer alternative methods of income generation, such as honey production or ecotourism. However, confidently making conservation recommendations for the region would require determining species' survival and reproductive rates in each vegetation type over several years, which was impossible in my dissertation. Besides completing these more long-term studies, future work can build upon my findings by expanding the range of species studied and both the spatial and temporal scales of the research. Further, determination of specific nest predators with the use of video cameras would shed light on how predator communities change across the landscape.

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