

THESIS

BODY SIZE, FIRST-YEAR BREEDING, AND EXTRA-PAIR PATERNITY IN AN ISLAND
ENDEMIC, THE ISLAND SCRUB-JAY

Submitted by

Michelle A. Desrosiers

Department of Biology

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Spring 2014

Master's Committee:

Advisor: Lisa M. Angeloni

Co-Advisor: Cameron K. Ghalambor

W. Chris Funk

T. Scott Sillett

Kevin R. Crooks

ABSTRACT

BODY SIZE, FIRST-YEAR BREEDING, AND EXTRA-PAIR PATERNITY IN AN ISLAND ENDEMIC, THE ISLAND SCRUB-JAY

Body size is a fundamental characteristic that shapes all aspects of an organism's biology. The advantages of large body size may include increased probability of territory acquisition, a critical component of fitness for species that require a territory to breed. Large body size, an indicator of quality, may also be advantageous to males in acquiring mates, including matings outside of a pair bond. Such advantages could be especially important in island systems because habitat saturation may result in strong intra-specific competition for territories, and females may be especially motivated to seek large extra-pair mates to increase the body size of their offspring. We tested the role of body size in determining the ability of an island-endemic bird, the Island Scrub-Jay *Aphelocoma insularis*, to acquire a territory and breed in their first spring, as well as to sire extra-pair offspring. We compared the body size of individuals that obtained a territory and bred to those that did not, as well as the body size of social fathers to the extra-pair sires to whom they lost paternity. We found that large body size was important in the siring of extra-pair young. However, body size did not predict the ability of male or female Island Scrub-Jays to acquire a territory and breed in their first year. We suggest that year-to-year variation in environmental conditions and chance may be more important than a large body size or weapon performance in early territory acquisition. Our study provides evidence for a mechanism, specifically female preference for a large body size in males, that supports the observed rates of extra-pair paternity, and demonstrates the general difficulty, even for individuals with a

relatively large body size, of acquiring a territory as a yearling in an island system with saturated habitat.

ACKNOWLEDGMENTS

This project would not have been possible without the help of many people. I'd like to first thank my committee members Drs. Lisa Angeloni, Cameron Ghalambor, Scott Sillett, Chris Funk and Kevin Crooks for their invaluable advice and feedback throughout the process. My research also benefited from the support of Scott Morrison, Christie Boser, and Jennifer Baker at The Nature Conservancy in California as well as Kate Faulkner at the National Park Service. I am indebted to Lyndal Laughrin for his behind the scenes work at the UC Santa Barbara Santa Cruz Island Reserve, Brian Guerrero for countless fishing expeditions and excellent Santa Cruz Island style barbeques, as well as his and Earl Ryder's tireless ingenuity in keeping our ancient field vehicles up and running. Rest in peace Aphelocomobile, you served well.

A small army of dedicated and enthusiastic field technicians made this work feasible. Thank you Sinéad Borchert, Mason Cline, Laura Duval, Michael Hague, Joanna Hatt, Chance Hines, Matt Gould, Alexi Kimiatek, Nora Livingston, Katrina Murböck, Courtenay Ray, and Liz White for hiking through knee deep floods, braving poison oak terror domes, and navigating spider webs of Chamise and Manzanita in search of valuable data points and nests. I'd like to especially thank Colin Woolley, who could have been exploring the wilds of South America, but instead let me tell him what to do for two years, and kept me grounded.

I would be remiss to not acknowledge the invaluable advice and input I received from my fellow island loving/ living graduate students. Luke Caldwell deserves a huge thanks for hiring me as a tech back in 2009, and beginning my education in all things Island Scrub-Jay. Katie Langin is a great friend and mentor. Helen Sofaer, Mario Pesendorfer and Adam Dillon shared good times and interesting scientific, as well as personal conversation out on Santa Cruz Island.

My parents deserve countless thanks for encouraging me to discover what made me tick: letting me run around barefoot, playing in the mud, hunting salamanders, and always ending up covered in bruises before family photos. Thanks for telling my kindergarten teacher to let me spend as much time as I wanted in the science corner.

Last but not least, I need to thank the Island Scrub-Jays themselves. Thank you for gracing me with your private warble songs when happy and your feet when I displeased you. It was an amazing and thought provoking 4 years, both as a technician, and a graduate student. I'll be back to visit.

TABLE OF CONTENTS

Abstract.....	ii
Acknowledgments.....	iv
Introduction.....	1
Methods.....	5
Results.....	12
Discussion.....	15
Tables.....	22
Figures.....	23
References.....	24
Appendix.....	35
Appendix tables.....	38
Appendix figures.....	39
Appendix references.....	40

INTRODUCTION

"Size dictates the characteristics of all living forms. It is the supreme and universal determinant of what any organism can be and can do." — John Tyler Bonner (2006)

An organism's body size fundamentally shapes all aspects of its biology (Thompson 1917; Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Bonner 2006). Some factors correlated with body size across taxa include physiological and metabolic rates (Bouteiller-Reuter & Perrin 2005; Bonner 2006), predator avoidance or defense (Christensen 1996; Arendt 2008; Geary *et al.* 2012; De Robertis *et al.* 2010), locomotor performance (Dial 2003), the timing and investment of energy in reproduction (Roff 1992; Stearns 1992), and mate choice (Darwin 1871; Andersson 1994). These factors and their interactions can determine the conditions favoring smaller or larger body sizes (Foster 1964; MacArthur & Wilson 1967; Van Valen 1973; Yeaton 1974; Case 1978; Sondaar 1986; Clegg & Owens 2002; Palkovacs 2003; Lomolino 2005).

The advantages of a large body size have been best documented in animals that exhibit sexual size dimorphism, where one sex, often the male, is larger and uses its size to monopolize breeding opportunities (Andersson 1994). In such cases, large body size often confers dominance in social hierarchies (Stamps & Krishnan 1994; Piper 1999; Jenssen *et al.* 2005; Martin & Moore 2008; Serrano-Meneses *et al.* 2007; Sacchi *et al.* 2009), and has been implicated in territory acquisition across a variety of taxa, including invertebrates (Martin & Moore 2008; Serrano-Meneses *et al.* 2007), amphibians (Mathis 1990, 1991), fish (Rowland 1989; Candolin & Voight 2001; Natsumeda *et al.* 2011), reptiles (Morrison *et al.* 2002; Jenssen *et al.* 2005), birds (Holmes *et al.* 1996; Keyser & Hill 2000; Marra & Holmes 2001; Mazerolle & Hobson 2002), and mammals (Bouteiller-Reuter & Perrin 2005; Iossa *et al.* 2008). The evolution of sexual size

dimorphism in these cases is often described as a form of intra-sexual selection due to greater fighting ability correlated with large body size (e.g. Haley *et al.* 1994; Alcock 1996), or the reluctance of a smaller adversary to escalate a contest where they may be more likely to be injured (Parker 1974).

A positive relationship between body size, dominance, and territory acquisition, however, is not universal. In some species, weapon performance, such as the bite force a jaw can exert (Lappin & Husak 2005; Husak *et al.* 2006), or length of residency in a location (Dale & Slagsvold 1995) are better correlated with success in contests than overall body size. A smaller body size may even be associated with dominance in some cases, due to greater locomotor ability and maneuverability in contests (Schulte-Hostedde & Millar 2002). Further, much research has been devoted to the positive influence of age and/or experience on dominance and territory acquisition, which often trumps the advantage of a larger size (Clutton-Brock 1988; Berdoy *et al.* 1995; Côté 2000; Coltman *et al.* 2002; Sergio *et al.* 2009a; Šárová *et al.* 2013). Studies are rare that compare individuals of known age and experience, but vary in body size, to test if size predicts dominance, territory acquisition, or the initiation of breeding.

Body size can also positively influence reproductive success, particularly when used as an indicator of quality in mate choice (Trivers 1972; Andersson 1994; Griffith *et al.* 2002; Swierk *et al.* 2012; Iossa *et al.* 2008). Even in socially monogamous species, which are expected to have reduced sexual selection for male body size (Dunn *et al.* 2001; Wiegmann & Nguyen 2006), large males may retain a fitness advantage through extra-pair matings, or copulations outside of the territorial pair bond (Weatherhead & Boag 1995; Lacey & Wiczorek 2001; Griffith *et al.* 2002; but see Neto *et al.* 2010). Thus a large body size has the potential to increase the fitness of males in socially monogamous species. However, in some species, body size

remains relatively unimportant in mate choice, and other hypothesized indicators of quality such as territory size, calling duration, horn length, and age are better correlated with reproductive success (Roithmair 1992; Roithmair 1994; Coltman *et al.* 2002; Ursprung *et al.* 2011). Thus, explaining existing variation in extra-pair paternity remains a complex problem in behavioral ecology (Griffith *et al.* 2002).

The advantages of a large body size may be pronounced in island systems for several reasons. Islands can exhibit habitat saturation (Komdeur 1992), and breeding territories may be limiting, which may result in a non-breeding portion of the population with some individuals never gaining the opportunity to breed (Newton 1994; Buston & Cant 2006). Thus, competition is expected to be especially strong on islands, which should select for traits, such as a large body size, that confer an advantage in competitive interactions (Atwood 1980b; Newton 1994; Buston & Cant 2006). Additionally, given the hypothesized advantages of a large body size in island competition, females of socially monogamous island species may be especially motivated to seek out males that are larger than their social mates as extra-pair mates to increase offspring body size and fitness (Griffith *et al.* 2002). However, the importance of extra-pair paternity in island systems is not clear, because of conflicting ideas about whether extra-pair mating should be relatively rare or common on islands as compared to mainland species. Island species typically have reduced genetic diversity (Frankham 1997), which reduces the benefit of extra-pair matings as a strategy to increase genetic diversity of offspring (Griffith 2000; Griffith *et al.* 2002; Krokene & Lifjeld 2000). However, island species often exist at higher densities than mainland species (Yeaton 1974; George 1987; Ricklefs & Lovette 1999), and experience reduced resources, both of which have the potential to increase the rate of extra-pair mating (Fridolfsson 1997; Charmantier & Blondel 2003).

We assessed the role of body size on initial territory acquisition and subsequent patterns of extra-pair paternity in the Island Scrub-Jay, *Aphelocoma insularis*, which is endemic to Santa Cruz Island, CA. The Island Scrub-Jay is socially monogamous, and mated pairs jointly defend a multi-purpose territory year round, potentially for life (Atwood 1980a; Curry & Delaney 2002). Island Scrub-Jays, which are larger in body size than their mainland congeners (Pitelka 1951), typically live as non-breeders and do not acquire a territory until a median age of four years (Atwood 1980a; Collins & Corey 1994), in contrast to Western Scrub-Jays, *A. californica*, and Florida Scrub-Jays, *A. coerulescens*, that acquire territories after one and two years, respectively (Woolfenden & Fitzpatrick 1996; Carmen 2004).

Given the potential for strong competition among Island Scrub-Jays for breeding territories, we hypothesized that body size is an indicator of individual quality and predicted a positive relationship between body size and early territory acquisition and extra-pair mating success. To test this hypothesis, we monitored yearling Island Scrub-Jays in their first spring, and compared the body size of individuals that did and did not obtain a breeding territory. We also assigned paternity to young within broods of territorial pairs and compared the body size of social fathers and extra-pair sires. Specifically, we predicted that Island Scrub-Jays that acquired and defended a territory and bred in their first breeding season would be larger than those that did not. We also predicted that males who fathered extra-pair offspring would be larger than the social mates that they cuckolded.

METHODS

Santa Cruz Island (34° 0' N, 119° 45' W), part of Channel Islands National Park, is 32 km off the coast of southern California and is the largest (249 km²) of the Channel Islands. The island has a Mediterranean climate characterized by cool, wet winters and hot, dry summers (Junak *et al.* 1995; Fisher *et al.* 2009). We worked on three study sites (see Caldwell *et al.* 2013) that ranged in size (226, 163, and 115 hectares) and encompassed a gradient of breeding habitat quality, from isolated oak chaparral interspersed in grassland to continuous oak chaparral. Fieldwork was conducted under permits from the USGS Bird Banding Lab (22665) and the California Department of Fish and Game (SC-6471, SC-11219), and under IACUC protocols approved by Colorado State University (08-314A-01, 09-045A-03, 12-3206A) and the Smithsonian Institution (11-28).

We captured Island Scrub-Jays from February through June 2009 – 2012 to collect morphological measurements necessary to test the role of size in early territory acquisition and breeding, as well as extra-pair paternity. We trapped birds using drop box traps and mist nets baited with peanuts. After capture, we used calipers to measure tarsus, exposed culmen, bill tip to nares, bill depth, and bill width to the nearest hundredth of a millimeter. We used a wing ruler to measure un-flattened wing chord to the nearest millimeter (Pyle 1997). We measured tarsus twice per capture on each individual, and the average of these measures was used in analyses. We collected 70 - 100 µl of blood from each jay via brachial venipuncture for genetic analysis and molecular sexing. Blood was stored in 1.5 mL of lysis buffer until DNA extraction.

Extra-pair paternity and size

During the breeding seasons (mid-February to late June) of 2010, 2011, and 2012, we monitored a minimum of 15 established breeding pairs on each study plot and attempted to find all nesting attempts to sample young for paternity analysis. We checked each nest every three days until it failed or successfully fledged young. A nest was considered successful if it was found empty, with the lining neat, edges partially flattened, and the parents were observed feeding young. A nest was considered to have failed if it was found empty with its lining damaged, with eggshells in or near the nest, or if the eggs were cold and the adults were seen building another nest (see Caldwell *et al.* 2013 for further details). We collected 50 – 100 μ l of blood from nestlings in accessible nests 11 to 13 days after hatching. 34 breeding pairs were sampled once, contributing a single brood to our dataset. Four breeding pairs were sampled twice with two broods across different years, and three pairs were sampled three times, with two broods in the same season (due to nest failure and subsequent re-nesting) and an additional brood in a different year.

We extracted DNA from blood samples with a Qiagen DNEasy Blood and Tissue Kit following the manufacturer's protocol and amplified 9 variable microsatellite loci (Langin *et al.* in prep). The microsatellites were amplified in 10 μ L multiplex reactions (with 2-5 loci per reaction) using QIAGEN's type-it microsatellite PCR kit and a Vapo-Protect Mastercycler 6321 (Eppendorf, Hauppauge, NY, USA). Loci in the same reaction were distinguished from one another by unique fluorescent labels or by pre-determined allele-size differences. The PCR products were run on an Applied BioSystems 3730xl DNA Analyzer, and the resulting electropherograms were scored automatically and checked manually with GeneMarker version 1.91 (SoftGenetics, State College, PA, USA). We dropped 3 nestlings from our parentage

analysis out of the total 158 sampled due to poor microsatellite amplification (five or less loci) and the resulting loss of power to resolve parentage unambiguously.

We used CERVUS version 3.0 to determine parentage and the presence of extra-pair paternity within broods (Kalinowski *et al.* 2007). CERVUS assigns parentage based on population-level allele frequencies and presents the results as the natural logarithm of the likelihood ratio, or LOD score. The likelihood ratio is calculated as the probability that a candidate male is the true parent of a given offspring, divided by the probability that the same male is not the true parent, multiplied over all loci for which genetic information is available. This approach allows for the possibility of low levels of typing error, as well as the possibility that not all sires have been sampled in the population. We assumed the territorial female of a sampled brood was the genetic mother, as no evidence of conspecific brood parasitism has been found in the species (Delaney 2003). With the 9 variable microsatellite loci used, the average probability that an unrelated parent could not be excluded when only the offspring genotype was known was 7.5×10^{-4} , the probability that an unrelated candidate male could not be excluded when the offspring and maternal genotype was specified was 2.1×10^{-5} , and the probability of not excluding an unrelated parent pair given only the genotype of the offspring was <0.00001 . The combined exclusionary power of the microsatellites we used is comparable to that achieved by other studies of parentage (Marshall *et al.* 1998; Delaney 2003).

Candidate fathers ($n = 231$ over the entire study) included all males sampled from fall 2009 through spring 2012 on the same study plot as the nestlings being assigned. We restricted our paternity assignment to individuals sampled on the same study plot because dispersal occurs before an individual's potential first breeding season (Langin *et al.* in prep), and territorial jays typically stay on the same territory for life (Atwood 1980b, Caldwell *et al.* 2013). CERVUS

requires the input of an estimated number of candidate males per plot, a value that is meant to incorporate both known possible sires and possible unknown sires not sampled. To estimate plot-specific numbers of candidate males, we took the area of each plot from Caldwell *et al.* (2013), and estimated habitat-specific densities from Sillett *et al.* (2012), divided by two.

We rejected CERVUS' assignment in 10 cases using a set of rules. First, we rejected an assignment if the candidate male was a full sibling of the offspring in question ($n = 8$ cases). Full siblings can have equal or slightly higher LOD scores than a true parent when a mother is not sampled ($n = 2$ of the 8 cases) or when the population exhibits high male philopatry (Marshall *et al.* 1998; Richardson *et al.* 2001), as in the Island Scrub-Jay (Langin *et al.* in prep.), and analyses are not separated by year (all 8 cases). Second, we rejected an assignment if the candidate male was not seen, or was presumed dead in the breeding season in which the offspring was sired ($n = 2$ cases). For these ten rejections we then assigned paternity when possible ($n = 8$ cases) to the next most likely male above the threshold needed for a 95% confident assignment.

To assess the role of body size in extra-pair mate choice, we used a paired *t*-test to compare the tarsus length of males that lost paternity (losers), to those that gained paternity (winners). Tarsus length for this analysis was the average of all measurements taken on an individual (range 1 – 5 captures, median 3), in many cases over multiple seasons.

Pair & breeding status of radio-tagged jays in their first breeding season

In order to follow first-year Island Scrub-Jays to determine their pair status and if they bred in their first spring, we fit hatch year jays with Lotek Pip Ag radio transmitters ($\leq 3\%$ of body mass). We fit 20 hatch year jays with transmitters in October 2011 and 20 in October 2012. Individuals outfitted with transmitters were the first 20 hatch year jays caught each fall in order

to maximize behavioral data collection. Transmitters were attached with a Rappole-Tipton harness (Rappole & Tipton 1991; Bowman & Aborn 2001) made of elastic thread and lasted 7 – 9 months.

We collected a point location confirmed by visual identification on each radio-tagged jay approximately every three days. After confirmation, we observed jays for five-minutes and noted pair behaviors (call and rattle exchanges joint foraging, joint perching, territory defense, and mate feeding), as well as agonistic behaviors (chases and displacement from a perch; see Curry & Delaney 2002 for a detailed description of behaviors). When possible, we recorded the identity of other individuals interacting with the focal jay. Jays captured in 2011 were followed using this protocol from the second week of February through the third week of May in 2012. Those captured in 2012 were tracked from the first week of October through the first week of December in 2012, and from the second week of March through the second week of May in 2013. Data collected in the fall of 2012 were used in a study of dominance behavior presented in the appendix. We classified a jay as being paired if we observed it engaging in pair behaviors with the same individual on multiple occasions throughout the breeding season. A paired jay was not classified as a breeder until we documented a complete nesting attempt (i.e., nest building, egg-laying, and nest attendance). We were confident in our ability to reliably assess breeding status throughout this entire first breeding season due to the frequency with which we tracked jays and checked any nests they built (every three days).

Territory acquisition, breeding, and size

To investigate the role of body size on territory acquisition and breeding, while controlling for age and experience, we compared the body size of Island Scrub-Jays that acquired a territory

and bred in their first spring with those that did not. Jays classified as territorial breeders included radio-tagged individuals that bred in 2012 and 2013, as well as individuals banded as a hatch year in 2009-2012 observed to breed in their first full spring. Jays classified as non-breeders included radio-tagged individuals that did not breed and birds of known sex banded as a hatch-year in 2009 – 2012 that were not observed as breeders. We used tarsus length as an index of body size (Rising & Somers 1989; Freeman & Jackson 1989). We did not use body mass because mass fluctuates temporally over the course of a day and a season in many avian species, including the Island Scrub-Jay (Atwood 1979), and our mass measurements of different individuals were taken over an approximately three month period. We used ANOVA to determine whether tarsus length varied with status (breeder or non-breeder), sex, and their interaction.

A structure that could be used as a weapon may also influence territory acquisition (Lappin & Husak 2005; Husak *et al.* 2006). We hypothesized that bills are important weapons for Island Scrub-Jays, because they are used as weapons in other birds, including other species of jay (Johnson 1988; Minguéz *et al.* 2001). When engaging in a physical contest, a jay will hold another individual on the ground and repeatedly peck at the back of the head and nape of the neck (Atwood 1980b; personal observation). We frequently noted missing feathers during routine banding procedures, presumably due to scar tissue in these areas. We used ANOVA to determine whether nares length, a measure of bill size, varied with status (breeder or non-breeder), sex, and their interaction to investigate a possible relationship between nares length and territory acquisition. We did not correct for body size in these analyses (e.g., by using residuals from a regression of nares length on body size), because there was no correlation between nares length and tarsus length in yearling male or female Island Scrub-Jays (males: $F_{1,95} = 0.66$, $P =$

0.42, $R^2 = 0.007$; females: $F_{1, 59} = 0.96$, $P = 0.33$, $R^2 = 0.02$). All statistical analyses were carried out in JMP version 10 (SAS institute 2012).

RESULTS

Extra-pair paternity and size

We determined whether parentage was within-pair or extra-pair for 153 nestlings from 53 broods (clutch size mean \pm SE: 3.67 ± 0.09 , range: 1-5 eggs) produced by 41 pairs. Six pairs (14.6%) had a brood that contained at least one extra-pair offspring. Seven broods (13.2%) contained extra-pair young, with the percentage of extra-pair young within those broods ranging from 25% to 100% (median = 50%; Figure 1). Twelve nestlings (7.8%) were extra-pair young. We were able to assign a sire at a 95% confidence level to 147 of 153 nestlings. The social males in the six unassigned cases (from two broods) were sampled, indicating extra-pair paternity from an un-sampled male. We assigned paternity to a specific extra-pair male in five broods that contained extra-pair young. Four of the extra-pair sires were neighboring territory holders; the territory status of the other sire was unknown. As predicted, cuckolding males had larger tarsi than the males they cuckolded ($t_{0.05} = 2.18$, $df = 4$, $P < 0.05$; winners: 47.31 ± 0.18 , losers: 46.67 ± 0.29 ; Figure 2).

Pair & breeding status of radio-tagged jays in their first breeding season

We were able to confidently assign status (breeder or non-breeder) to 27 out of 40 radio-tagged Island Scrub-Jays. Eleven of 27 yearling jays that we radio-tracked engaged in some form of reproductive behavior in their first breeding season. Two males that successfully defended a small territory were able to build a nest and mate (Table 1). Both nests were depredated. These two young pairs did not build new nests, even though established pairs often re-nest following nest failure (Caldwell *et al.* 2013). The remaining nine individuals (8 males, 1 female) formed pairs but did not breed. Seven (6 males, 1 female) established and defended a small territory; the

other two, both male, were unable to establish and defend a territory (Table 1). The remaining 16 jays that were not observed engaging in reproductive behavior were often detected while foraging alone in dense vegetation, although they occasionally associated with other jays. These associations were transient (i.e., they were seen with the same individual on fewer than three occasions over less than nine days) and therefore not indicative of long-term pair bonding. We could not determine the status of 13 Island Scrub-Jays that received radio transmitters. Seven were depredated prior to their first spring; one died in fall 2011, and the remaining six died over the winter of 2012 – 2013. Three jays lost transmitters prior to their first breeding season, two transmitters' batteries failed, and we never received a signal from one jay, either due to battery failure or the movement of the jay out of range of the study plots (Table 1).

Territory acquisition, breeding, and size

Contrary to predictions, we did not find that body size, or our measure of weapon size, were related to territory acquisition and breeding in male or female yearling Island Scrub-Jays. We found no difference in tarsus length between individuals that acquired a territory and bred as yearlings and those that did not ($F_{3, 177} = 38.46$, $P = 0.53$; male breeders = 47.01 ± 0.26 , male non-breeders = 46.91 ± 0.10 ; female breeders = 45.45 ± 0.29 , female non-breeders = 45.28 ± 0.13) and we found no difference in weapon size, specifically bill length, as measured from nares to tip, between yearling territorial breeders and non-breeders ($F_{3, 178} = 47.40$, $P = 0.29$; male breeders = 24.96 ± 0.26 , male non-breeders = 24.51 ± 0.10 ; female breeders = 22.79 ± 0.30 , female non-breeders = 22.78 ± 0.13). Sex was a predictor of both tarsus length ($F_{3, 177} = 38.46$, $P < 0.0001$) and bill length ($F_{3, 178} = 38.46$, $P < 0.0001$), which was not unexpected given sexual size dimorphism in the Island Scrub-Jay (Pitelka 1951). We found no significant interactions

between sex and status on tarsus length ($F_{3,177} = 38.46$, $P = 0.85$), or bill length ($F_{3,178} = 38.46$, $P = 0.32$).

DISCUSSION

The conditions that result in a positive relationship between body size and fitness have important implications for understanding the evolution of body size (Brown *et al.* 1993). In many species, larger individuals are dominant in social groups, giving them greater access to resources such as food, shelter, or mates, and thus greater fitness (Andersson 1994; Piper 1999; Robertson 1996). We found that extra-pair paternity in the Island Scrub-Jay, but not first year breeding, was positively associated with body size. We expected body size or weapon size to influence the ability of young Island Scrub-Jays to acquire and defend territories in this saturated island system, yet we did not detect such patterns, suggesting other factors may be more important. Our paternity findings, however, did support our predictions and the previous literature suggesting that body size can provide a mating advantage to males, even in a socially monogamous species, where extra-pair matings have the potential to skew reproductive success (Weatherhead & Boag 1995; Dunn *et al.* 2001; Lacey & Wieczorek 2001; Griffith *et al.* 2002; Wiegmann & Nguyen 2006).

Body size and extra-pair paternity

Genetic monogamy is the exception rather than the rule in avian mating systems, with over 90% of species exhibiting some level of extra-pair paternity, or mating outside of the pair bond (Griffith *et al.* 2002). Among socially monogamous avian species, an average of 11.1% of offspring and 18.7% of broods have extra-pair paternity (Griffith *et al.* 2002). The rate of extra-pair paternity we detected in the socially monogamous Island Scrub-Jay (7.8% of offspring, 13.2% of broods) is therefore relatively low. It is also lower than the Western Scrub-Jay (21.4%

of offspring; Delaney 2003), but higher than the cooperatively breeding Florida Scrub-Jay (0%; Townsend *et al.* 2011).

Studies of extra-pair paternity provide conflicting evidence for if and how rates of extra-pair paternity differ between island and mainland bird species. Founder events and genetic drift in small island populations decrease genetic diversity (Frankham 1997), thereby reducing the benefit to females of extra-pair matings as a strategy to maximize the genetic diversity of their offspring (Griffith 2000; Griffith *et al.* 2002; Krokene & Lifjeld 2000). The lower extra-pair paternity in the Island Scrub-Jay compared to the Western Scrub-Jay is consistent with this hypothesis. However, lower rates of extra-pair paternity are not always found in island populations known to have reduced genetic diversity. In fact, some island species exhibit greater levels of extra-pair paternity than their mainland counterparts (Fridolfsson 1997) even when genetic diversity is lower in the island population (Charmantier & Blondel 2003). The disproportionate influence of high breeding density and resource limitation are suggested mechanisms that may increase rates of extra-pair paternity on islands in the face of reduced genetic diversity (Fridolfsson 1997; Charmantier & Blondel 2003).

Theory predicts that a female must acquire benefits to engage in extra-pair matings, especially if they risk losing male parental care as a result (Dixon *et al.* 1994; Perlut *et al.* 2012). Benefits can be direct, such as access to resources, or indirect, such as maximizing the genetic diversity or genetic quality of their offspring (Griffith *et al.* 2002). We found that female Island Scrub-Jays engaged in extra-pair matings with males that were larger than their social mate (Figure 2). If body size reflects underlying genetic quality, then these results would be consistent with the hypothesis that females seek “good genes” for their offspring by mating with males who present phenotypes (e.g., large body size) that are indicators of quality (Trivers 1972; Moller

1988; Westneat *et al.* 1990; Birkhead & Moller 1992). Our results suggest that being a large male Island Scrub-Jay can increase an individual's reproductive success through extra-pair matings. However, extra-pair matings may not always result in increased male reproductive success. In some species, males that engage in extra-pair matings suffer a loss of paternity in their own nest (Andersson 1994; Webster *et al.* 1995; Churchill & Hannon 2010). Concurrent loss of paternity is expected in systems where the "rules" governing why females engage in extra-pair matings apply equally to all females (i.e., females engage in extra-pair matings as insurance against mate infertility). This is in contrast to situations where females are seeking good genes, which tend to provide disproportionate paternity benefits to high quality males. High quality males are able to gain extra-pair paternity for themselves, but have mates that are unlikely to seek matings elsewhere (Kokko & Morrell 2005). We see this latter pattern in our paternity data. Large male Island Scrub-Jays were able to gain extra-pair paternity, but we did not find evidence of concurrent loss of paternity in their own nests.

Body size and the ability to breed in the first year

Island Scrub-Jays, which are physiologically capable of reproducing in their first breeding season (Atwood 1980b; Caldwell *et al.* 2013), exhibited a wide range of reproductive behaviors in their first year (Table 1). Many individuals did not engage in any breeding behavior, some formed a pair bond and jointly defended a small territory, and a few built nests and produced eggs (Table 1). This gradient of breeding behavior is similar to that observed in young Western Scrub-Jays (Carmen 2004), but differs from the cooperative breeding system of Florida Scrub-Jays and a population of Western Scrub-Jays in Oaxaca, Mexico, where young will forego their own reproduction and stay on their natal territory to help raise siblings (Burt & Peterson

1993; Wolfenden & Fitzpatrick 1984). The formation of breeding pair relationships prior to territory acquisition has also been noted in other non-breeding birds (e.g., oystercatchers, *Haematopus ostralegus*; Heg *et al.* 2000). A common strategy of non-breeding birds is to spend time on the territories of breeding individuals, either waiting for a vacancy, or attempting to evict an owner (Zack & Stutchbury 1992; Tobler & Smith 2004). This pattern is especially prevalent in long-lived species that hold year-round territories in saturated habitat (e.g., tropical species), or that migrate with high site fidelity (Zack & Stutchbury 1992; Duca & Marini 2014). Yearling Island Scrub-Jays that acquired a territory and bred often did so on the borders of established territories, suggesting that they employ a strategy similar to other long-lived species that experience habitat saturation by spending time prospecting near established pairs. Other non-breeding tactics of avian species include membership in non-breeding flocks (e.g., some colonial seabirds; Hudson 1985). These flocks can include dominance hierarchies, with locally high-ranking individuals most likely to acquire a vacancy (e.g., Magpie, *Pica pica*; Eden 1987).

Our inability to detect a relationship between body size and early territory acquisition in the Island Scrub-Jay is surprising given that we expected a benefit of large body size due to habitat saturation, which should select for traits that confer a competitive advantage (Atwood 1980b; Newton 1994; Buston & Cant 2006). Nevertheless, it is possible that a large body size is advantageous in territory acquisition for young Island Scrub-Jays, but properties of our data set may have obscured the pattern. First, we may have underestimated the number of breeders by classifying some breeders incorrectly as non-breeders. Individuals that were undetected on territories were classified as non-breeders, but may have established territories out of the bounds of our study area. Additionally, due to the rarity of first year breeding the number of breeders was low (14 males and 11 females), reducing our power to detect a pattern. Ideally we would be

able to compare a larger sample of known territorial, breeding individuals to known non-territorial, non-breeding individuals.

Factors other than body size may play a larger role in territory acquisition and breeding in a jay's first year of life. It is possible that the inexperience of young Island Scrub-Jays prevents even those with a relatively large body size from acquiring a territory and breeding as a yearling since they are likely competing with older birds for a territory (Atwood 1980a; Collins & Corey 1994). This may be especially likely if older individuals direct greater aggression towards younger individuals regardless of size (Coté 2000). Additionally, other factors, including familiarity with the terrain and chance vacancies, likely play a role in territory acquisition (Collins & Corey 2005; Mudry 2008). Vacancies are filled fast, often within days, especially within the breeding season (Collins & Corey 2005; personal observation), which may favor jays that are familiar with the area and its established pairs, or that happen upon an opening, regardless of body size (Zack & Stutchbury 1992). If one member of a mating pair dies and the surviving individual does not replace its mate quickly, two Island Scrub-Jays already interacting as a pair may force out the previously established breeder (Collins & Corey 2005; personal observation).

Different years present different resource availability for young jays, which apparently influences their ability to survive their first winter and possibly obtain a territory. Wetter years may result in greater densities of food resources for egg laying and feeding young (Denac 2006), and young jays may be able to nest in areas that would be unsuitable in dryer years. We found that yearling birds bred in apparently unoccupied territory sites in 2010 ($n = 11$) and 2011 ($n = 8$), years that were preceded by relatively wet rainy seasons (Western Regional Climate Center). In contrast, 2012 only had two yearlings attempt to breed and 2013, a drought year, had none.

The winter rainy season of 2012-2013 was the driest of our radio-tracking study, and we noted the most deaths due to predation in our population of radio-tagged jays that winter ($n = 6$ out of 20; Table 1). Jays may engage in risky foraging behavior when nutritionally stressed, as in drought years, putting them at greater risk of being depredated (Sweitzer 1996; Bateson 2002).

Conclusions

Island taxa often exhibit differences in body size compared to closely related mainland species (Foster 1964; Case 1978; Sondaar 1986; Lomolino 2005). Some taxa tend to become larger on islands, while others become smaller, due to a variety of interacting factors such as reduced or non-existent emigration, reduced species diversity, changes in competition and predation, as well as resource limitation (Foster 1964; MacArthur & Wilson 1967; Yeaton 1974; Palkovacs 2003). Population densities are often high on islands (Yeaton 1974; George 1987; Ricklefs & Lovette 1999), leading to limited habitat and elevated intraspecific competition, where large body size can confer a dominance advantage (Robinson-Woolrath & Owens 2003), and smaller individuals may be excluded from breeding (Newton 1994; Buston & Cant 2006). Given the saturated breeding habitat of Santa Cruz Island (Atwood 1980b; Caldwell *et al.* 2013), and the later median age of first breeding (Atwood 1980a), we predicted that a large body size would be advantageous in territory acquisition and breeding in yearling Island Scrub-Jays. We did not find evidence of this pattern, but our hypothesis warrants further investigation with confident measures of non-breeders over a longer time scale to better evaluate the role of temporal variables, such as rainfall, on body size and suitability of habitat for early breeding.

Future research that would further our understanding of the correlates of extra-pair paternity rates could assess the relationship between age, experience and extra-pair mating in the

Island Scrub-Jay. A larger sample of broods and of precisely aged males would lend insight as to if young males are being cuckolded more often than older males, or even if older males may tolerate the bordering territories of young males in order to cuckold them (Greene *et al.* 2000). Additionally, older, more experienced males may simply be more skilled at gaining extra-pair matings (Weatherhead & Boag 1995).

How body size and reproductive success are inter-related in the Island Scrub-Jay is almost definitely more complicated than simply acquiring a territory or gaining extra-pair matings. For example, it is possible that larger individuals may be able to acquire higher quality territories (Sergio *et al.* 2009b) that have reduced predation risk (Caldwell *et al.* 2013). Territories with greater vegetation height and complexity, which leads to better nest concealment (Caldwell *et al.* 2013), may be more desirable territories that only larger individuals can acquire. Similarly, larger birds may defend their nest against predators more aggressively (Larsen *et al.* 1996), which could also increase their lifetime reproductive success. Though additional future research is needed, our study contributes empirical findings to the body of literature investigating the evolution of body size and its contribution to fitness, both through territory acquisition and extra-pair mating success.

TABLES

Table 1: Status of the 40 radio-tagged Island Scrub-Jays during the spring of 2012 and 2013. Jays were tagged in the fall of 2011 and 2012 as hatch years.

<i>Hatch year 2011</i>	Males	Females
Breeder	2	-
Paired & Territorial	5	1
Paired	5	-
Non-breeder	2	5
Depredated	-	1
Alive, dropped/ bad transmitter	-	2
Unknown	-	-
<i>Hatch year 2012</i>		
Breeder	-	-
Paired & Territorial	1	-
Paired	-	-
Non-breeder	6	3
Depredated	5	1
Alive, dropped/ bad transmitter	1	2
Unknown	1	-

FIGURES

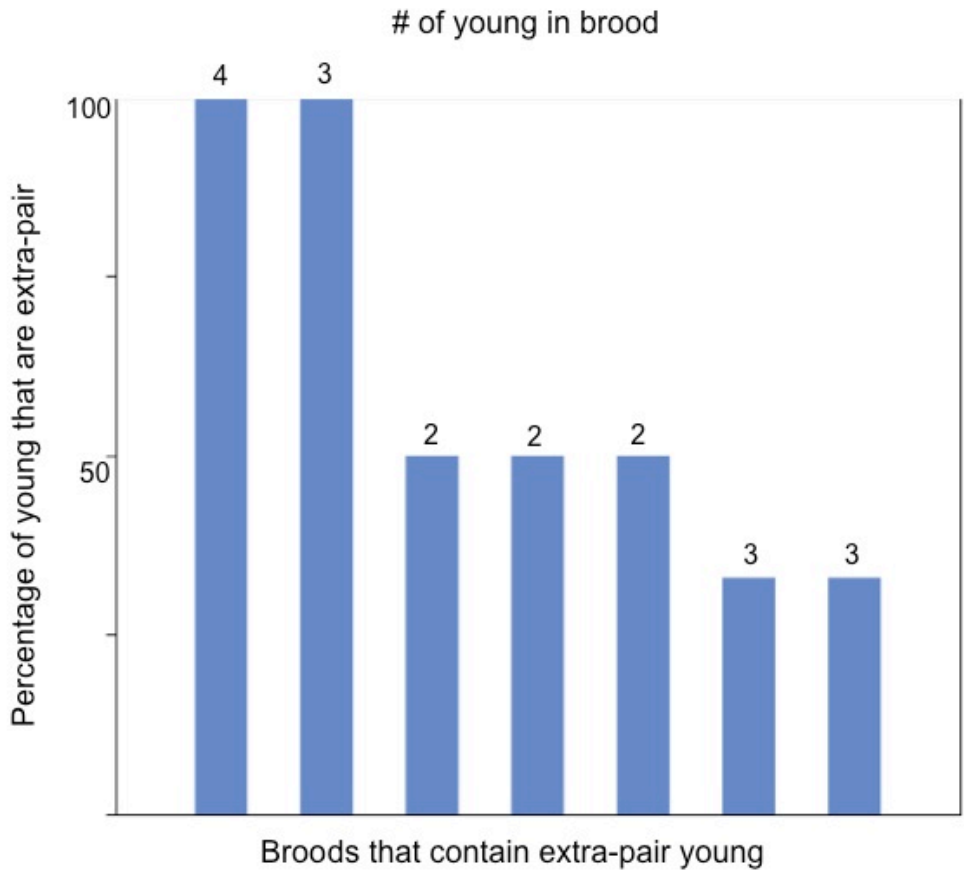


Figure 1: Percentage of within-pair and extra-pair offspring in broods containing extra-pair offspring (n = 7).

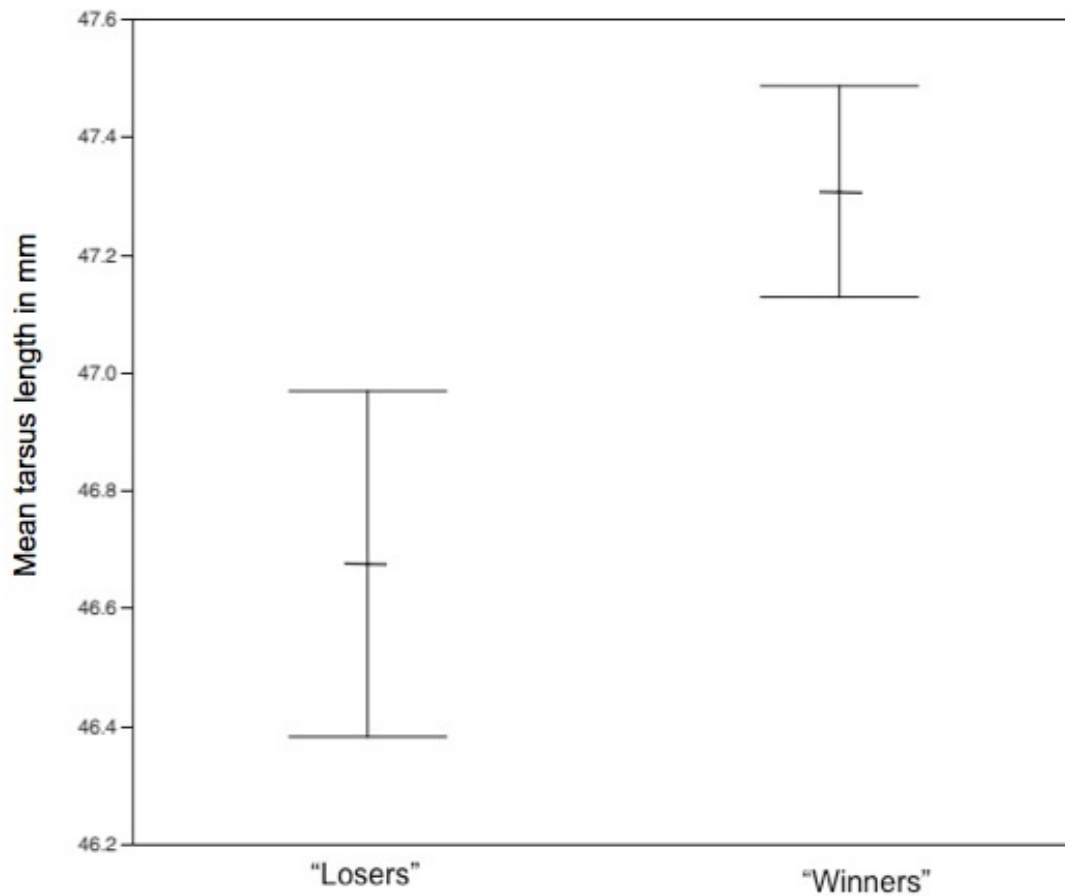


Figure 2: Mean tarsus lengths of the 5 pairs of extra-pair paternity “winners” and “losers” that were compared. Bars represent one standard error around the mean.

REFERENCES

- Alcock, J. 1996. The relation between male body size, fighting, and mating success in Dawson's burrowing bee, *Amegilla dawsoni* (Apidae, Apiae, Anthophorini). *Journal of Zoology* 239: 663-674.
- Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton, NJ, USA.
- Arendt, J. D., 2009. Influence of sprint speed and body size on predator avoidance in New Mexican spadefoot toads (*Spea multiplicata*). *Oecologia* 159:455-461.
- Atwood, J. L. 1979. Body weights of the Santa Cruz Island Scrub Jay. *North American Bird Bander* 4: 148-153.
- Atwood, J. L. 1980a. Breeding biology of the Santa Cruz Island Scrub Jay. In Power, D. M. (ed.). *The California Islands: proceedings of a multidisciplinary symposium*, pp. 675-688. Santa Barbara Museum of Natural History, Santa Barbara, CA, USA.
- Atwood, J. L. 1980b. Social interactions in the Santa Cruz Island Scrub Jay. *The Condor* 82: 440-448.
- Bateson, M. 2002. Recent advances in our understanding of risk-sensitive foraging preferences. *Proceedings of the Nutrition Society* 61: 509-516.
- Berdoy, M., Smith, P. and MacDonald, D. 1995. Stability of social status in wild rats: Age and the role of settled dominance. *Behaviour* 132: 193-212.
- Birkhead, T. and A. Moller. 1992. Faithless female seeks better genes. *New Scientist* 135: 34-38.
- Bonner, J.T. 2006. *Why size matters: From bacteria to blue whales*. Princeton University Press: Princeton, New Jersey, USA.
- Bouteiller-Reuter, C., and N. Perrin. 2005. Sex-specific selective pressures on body mass in the greater white-toothed shrew, *Corcidura russula*. *Journal of Evolutionary Biology* 18: 290-300
- Bowman, R., and D. A. Aborn. 2001. Effects of different radio transmitter harnesses on the behavior of Florida scrub-jays. *Florida Field Naturalist* 29: 81-86.
- Brown, J.H., Marquet, P.A., Taper, M.L. 1993. Evolution of body size: consequences of an energetic definition of fitness. *The American Naturalist* 142: 573-584.
- Burt, D. B., and A. T. Peterson. 1993. Biology of cooperative-breeding scrub jays (*Aphelocoma coerulescens*) of Oaxaca, Mexico. *The Auk* 110: 207-214.
- Buston, P. M., and M. A. Cant. 2006. A new perspective on size hierarchies in nature: patterns, causes, and consequences. *Oecologia* 149: 362-372.

- Calder, W. A. 1984. Size, Function, and Life History. Harvard University Press, Cambridge, MA, USA.
- Caldwell, L., V. J. Bakker, T. S. Sillett, M. A. Desrosiers, S. A. Morrison, L. M. Angeloni. 2013. Reproductive ecology of the Island Scrub-Jay. *The Condor* 115: 603-613.
- Candolin, U., and H-R. Voight. 2001. Correlation between male size and territory quality: consequence of male competition or predation susceptibility? *Oikos* 95: 225-230.
- Carmen, W. J. 2004. Noncooperative breeding in the California Scrub-Jay. *Studies in Avian Biology* No. 28. Cooper Ornithological Society
- Case, T. J. 1978. A general explanation for insular body size trends in terrestrial vertebrates. *Ecology* 59: 1-118.
- Charmantier, A. and J. Blondel. 2003. A contrast in extra-pair paternity levels on mainland and island populations of Mediterranean blue tits. *Ethology* 109: 351-363.
- Churchill, J. L. and S. J. Hannon. 2010. Off-territory movement of male American Redstarts (*Setophaga ruticilla*) in a fragmented agricultural landscape is related to song rate, mating status, and access to females. *Journal of Ornithology* 151: 33-44.
- Christensen, B. 1996. Predator foraging capabilities and prey antipredator behaviours: pre-versus postcapture constraints on size-dependent predator-prey interactions. *Oikos* 76: 368-380.
- Clegg, S. M., and I. P. F. Owens. 2002. The 'island rule' in birds: medium body size and its ecological explanation. *Proceedings of the Royal Society B* 269: 1359-1365.
- Clutton-Brock, T. H. 1988. Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems. The University of Chicago Press, Chicago, IL, USA.
- Collins, C. T., and K. A. Corey. 1994. Delayed breeding in the Santa Cruz Island Scrub Jay: why not be cooperative? *Proceedings of the Fourth California Islands Symposium* (W. L. Halvorson, and G. J. Maender, Editors). Santa Barbara Museum of Natural History, Santa Barbara, CA, USA.
- Collins, C. T., and K. A. Corey. 2005. Territory acquisition in Island Scrub-Jays: How to become a breeder. *Proceedings of the Sixth California Islands Symposium* (D. K. Garcelon and C. A. Schwemm, Editors). Institute for Wildlife Studies, Arcata, CA, USA.
- Coltman, D. W., M. Festa-Bianchet., J. T. Jorgenson, and C. Strobeck. 2002. Age-dependent sexual selection in Bighorn Rams. *Proceedings of the Royal Society B* 269: 165-172.
- Côté, S. D. 2000. Dominance hierarchies in female mountain goats: stability, aggressiveness and determinants of rank. *Behaviour* 137: 1541-1566.

Curry, R. L. and K. S. Delaney. 2002. Island Scrub-Jay (*Aphelocoma insularis*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online:

<http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/713>

Dale, S., and T. Slagsvold. 1995. Female contests for nest sites and mates in the Pied Flycatcher, *Ficedula hypoleuca*. *Ethology* 99: 209-222.

Darwin, C. 1871. The descent of man, and selection in relation to sex. 1st ed., John Murray, London, England.

Delaney, K. S., 2003. Evolution and behavior of Island Scrub-Jays (*Aphelocoma insularis*), Western Scrub-Jays (*Aphelocoma californica*), and Sage Grouse (*Centrocercus urophasianus*) Ph.D. dissertation, University of California Los Angeles, Los Angeles, CA, USA.

Denac, D. 2006. Resource-dependent weather effect in the reproduction of the White Stork, *Ciconia ciconia*. *Ardea* 94: 233-240.

DeRobertis, A. Jaffe, J.S., Ohman, M.D. Visual predation risk and the timing of vertical migration in zooplankton. *Limnology and oceanography* 45: 1838-1844.

Dial, K. P. 2003. Evolution of avian locomotion: correlates of flight style, locomotor modules, nesting biology, body size, development, and the origin of flapping flight. *The Auk* 120: 941-952.

Dixon, A., D. Ross, S. L. C. O'Malley and T. Burke. 1994. Paternal investment inversely related to degree of extra-pair paternity in the reed bunting. *Nature* 371: 698-700.

Duca, C. and M. A. Marini. 2014. Territorial system and adult dispersal in a cooperative-breeding tanager. *The Auk* 131: 32-40.

Dunn, P. O., L. A. Whittingham and T. E. Pitcher. 2001. Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution* 55: 161-175.

Eden, S. F. 1987. Dispersal and competitive ability in the magpie: an experimental study. *Animal Behaviour* 35: 764-772.

Fisher, D. T., C. J. Still, A. P. Williams. 2009. Significance of summer fog and overcast for drought stress and ecological functioning of coastal California endemic plant species. *Journal of Biogeography* 36: 783-799.

Foster, J. B., 1964. Evolution of mammals on islands. *Nature* 202: 234-235.

Frankham, R. 1997: Do island populations have less genetic variation than mainland populations? *Heredity* 78: 311-327.

- Freeman, S. and W. M. Jackson. 1990. Univariate metrics are not adequate to measure avian body size. *The Auk* 107: 69-74.
- Fridolfsson, A., U. B. Gyllensten and S. Jakobsson. 1997. Microsatellite markers for paternity testing in the willow warbler *Phylloscopus trochilus*: high frequency of extra-pair young in an island population. *Hereditas* 126: 127-132.
- Geary, D. H., E. Hoffmann, I. Magyar, J. Freiheit and D. Padilla. 2012. Body size, longevity, and growth rate in Lake Pannon melanopsid gastropods and their predecessors. *Paleobiology* 38: 554-568.
- George, T. L. 1987. Greater land bird densities on island vs. mainland: relation to nest predation level. *Ecology* 68: 1393-1400.
- Greene, E., B. E. Lyon, V. R. Muehler, L. Ratcliffe, S. J. Oliver, and P. T. Boag. 2000. Disruptive sexual selection for plumage coloration in a passerine bird. *Nature* 407: 1000-1003.
- Griffith, S. C., I. P. F. Owens, K. A. Thuman. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology* 11: 2195-2212.
- Griffith, S. C. 2000. High fidelity on islands: a comparative study of extra pair paternity in passerine birds. *Behavioral Ecology* 11: 265-273.
- Haley, M. P., C. D. Deutsch and B. J. Le Boeuf. 1994. Size, dominance and copulatory success in male northern elephant seals, *Mirounga angustirostris*. *Animal Behaviour* 48: 1249-1260.
- Heg, D., B. J. Ens, H. P. Van Der Jeugd and L. W. Bruinzeel. 2000. Local dominance and territorial settlement of non-breeding oystercatchers. *Behaviour* 137: 473-530.
- Holmes, R. T., P. P. Marra and T. W. Sherry. 1996. Habitat-specific breeding demography of Black-throated Blue Warblers (*Dendroica caerulescens*): implications for population dynamics. *Journal of Animal Ecology* 65: 183-195.
- Hudson, P. J. 1985. Population parameters for the Atlantic Alcidae. In *The Atlantic Alcidae* (D. N. Nettleship & T. R. Birkhead, Editors). Academic Press, London, England. pp. 233-261.
- Husak, J. F., A. K. Lappin, S. F. Fox and J. A. Lemos-Espinal. 2006. Bite-force performance predicts dominance in male venerable collared lizards (*Crotaphytus antiquus*). *Copeia* 2006: 301-306.
- Iossa, G., C. D. Soulsbury, P. J. Baker and S. Harris. 2008. Body mass, territory size, and life-history tactics in a socially monogamous canid, the red fox, *Vulpes vulpes*. *Journal of Mammalogy* 89: 1481-1490.

Jenssen, T. A., K. R. Decourcy, J. D. Congdon. 2005. Assessment in contests of male lizards (*Anolis carolinensis*): how should smaller males respond when size matters? *Animal Behaviour* 69: 1325-1336.

JMP, Version 10.0.0. SAS Institute Inc., Cary, NC, 1989-2012.

Johnson, K. 1988. Sexual Selection in pinyon jays I: female choice and male-male competition. *Animal Behaviour* 36: 1038-1047.

Junak, S., T. Ayers, R. Scott, D. Wilken and D. Young. 1995. A Flora of Santa Cruz Island. California Native Plant Society, Sacramento, CA, USA.

Kalinowski, S. T., M. L. Taper and T. C. Marshall. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology* 16: 1099-1106.

Keyser, A. J. and G. E. Hill. 2000. Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks. *Behavioral Ecology* 11: 202-209.

Kokko, H. and L. J. Morrell. 2005. Mate guarding, male attractiveness, and paternity under social monogamy. *Behavioral Ecology* 16: 724-731.

Komdeur, J. 1992. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature* 358: 493-495.

Krokene, C. and J. T. Lifjeld. 2000. Variation in the frequency of extra-pair paternity in birds: a comparison of an island and a mainland population of Blue Tits. *Behaviour* 13: 1317-1330.

Lacey, E. A. and J. R. Wieczorek. 2001. Territoriality and male reproductive success in arctic ground squirrels. *Behavioral Ecology* 12: 626-632.

Langin, K. M., T. S. Sillet, W. C. Funk, S. Morrison, M. A. Desrosiers, and C. K. Ghalambor. Islands within an island: repeated adaptive divergence in a single population. *In preparation*

Lappin, A. K., J. F. Husak. 2005. Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *The American Naturalist* 166: 426-436.

Larsen, T., T. A. Sordahl and I. Byrkjedal. 1996. Factors related to aggressive nest protection behaviour: a comparative study of Holarctic waders. *Biological Journal of the Linnean Society* 58: 409-439.

Lomolino, M. V. 2005. Body size evolution in insular vertebrates: generality of the island rule. *Journal of Biogeography* 32: 1683-1699.

- MacArthur, R. H. and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ, USA.
- Marra, P. P. and R. T. Holmes. 2001. Consequences of dominance-mediated habitat segregation in American Redstarts during the nonbreeding season. *The Auk* 118: 92-104.
- Marshall, T. C., J. Slate, L. E. B. Kruus, and J. M. Pemberton. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology* 7: 639-655.
- Martin, A. L. and P. A. Moore. 2008. The influence of dominance on shelter preference and eviction rates in the crayfish, *Orconectes rusticus*. *Ethology* 114: 351-360.
- Mathis, A. 1990. Territoriality in a terrestrial salamander: The influence of resource quality and body size. *Behaviour* 112: 162-175.
- Mathis, A. 1991. Territories of male and female terrestrial salamanders: costs, benefits, and intersexual spatial associations. *Oecologia* 86: 433-440.
- Mazerolle, D. F. and K. A. Hobson. 2002. Physiological ramifications of habitat selection in territorial male Ovenbirds: Consequences of landscape fragmentation. *Oecologia* 130: 356-363.
- Minguez, E., J. Belliure and M. Ferrer. 2001. Bill size in relation to position in the colony in the Chinstrap Penguin. *The International Journal of Waterbird Biology* 24: 34-38.
- Moller, A. P. 1988. Badge size in the house sparrow, *Passer domesticus*. Effects of intrasexual and intersexual selection. *Behavioral Ecology and Sociobiology* 22: 373-378.
- Morrison, S. F., S. Keogh and A. W. Scott. 2002. Molecular determination of paternity in a natural population of the multiply mating polygynous lizard *Eulamprus heatwolei*. *Molecular Ecology* 11: 535-545.
- Mudry, N. 2008. Activity space and movement patterns of prebreeding Island Scrub-Jays (*Aphelocoma insularis*) on Santa Cruz Island, California. MS Thesis. California State University, Long Beach, Long Beach, CA, USA.
- Natsumeda, T., S. Mori and M. Yuma. 2012. Size-mediated dominance and aggressive behavior of male Japanese fluvial sculpin *Cottus pollux* (Pisces: Cottidae) reduce nest-site abundance and mating success of conspecific rivals. *Journal of Ethology* 30: 239-245.
- Newton, I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. *Biological Conservation* 70: 265-276.
- Neto, J. M., B. Hansson and D. Hasselquist. Low frequency of extra-pair paternity in Savi's Warblers (*Locustella luscinioides*). *Behaviour* 147: 1413-1429.

- Palkovacs, E. P. 2003. Explaining adaptive shifts in body size on islands: a life history approach. *Oikos* 103: 37-44.
- Parker, G. A. 1974. Assessment strategy and the evolution of fighting behavior. *Journal of Theoretical Biology* 47: 223-243.
- Perlut, N. G., L. M. Kelly, N. J. Zalik and A. M. Strong. 2012. Male Savannah Sparrows provide less parental care with increasing paternity loss. *Northeastern Naturalist* 19: 335-344.
- Peters, R. H. 1983. *The Ecological Implications of Body Size*. Cambridge University Press, New York, NY, USA.
- Piper, W. H., K. B. Tischler, M. Klich. 1999. Territory acquisition in loons: the importance of take-over. *Animal Behaviour* 59: 385-394.
- Pitelka, F. A. 1951. Speciation and ecological distribution of American jays of the genus *Aphelocoma*. *University of California Publications in Zoology* 50: 195-464.
- Pyle, P. 1997. *Identification Guide to North American Birds, Part I: Columbidae to Ploceidae*. Slate Creek Press, Bolinas, CA, USA.
- Rappole, J. H. and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62: 335-337.
- Richardson, D.S., F. L. Jury, K. Blaakmeer, J. Komdeur, and T. Burke. 2001. Parentage assignment and extra-group paternity in a cooperative breeder: the Seychelles warbler (*Acrocephalus sechellensis*). *Molecular Ecology* 10: 2263-2273.
- Ricklefs, R. E. and I. J. Lovette. 1999. The roles of island area *per se* and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. *Journal of Animal Ecology* 68: 1142-1160.
- Rising, J. D. and K. M. Somers. 1989. The measurement of overall body size in birds. *The Auk* 106: 666-674.
- Robinson-Wolrath, S. I. and I. P. F. Owens. 2003. Large size in an island-dwelling bird: intraspecific competition and the dominance hypothesis. *Journal of Evolutionary Biology* 16: 1106-1114.
- Robertson, D. R. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. *Ecology* 77: 885-899.
- Roithmair, M. E. 1992. Territoriality and male mating success in the dart-poison frog, *Epipedobates femoralis* (Dendrobatidae, Anura). *Ethology* 92: 331-343.

- Roithmair, M. E. 1994. Male territoriality and female mate selection in the dart-poison frog, *Epipedobates femoralis* (Dendrobatidae, Anura). *Copeia* 1994: 107-115.
- Roff, D. A. 1992. The evolution of life histories: Theory and analysis. Chapman & Hall, New York, NY, USA.
- Rowland, W. J. 1989. The effects of body size, aggression and nuptial coloration on competition for territories in male threespine sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour* 37: 282-289.
- Sacchi, R., F. Pupin, A. Gentili, D. Rubolini, S. Scali, M. Fasola, and P. Galeotti. 2009. Male-male combats in a polymorphic lizard: residency and size, but not color, affect fighting rules and contest outcome. *Aggressive Behavior* 35: 274-283.
- Šárová, R., M. Špinka, I. Stěhulová, F. Caecero, M. Šimečková, and R. Kotrba. 2013. Pay respect to the elders: age, more than body mass, determines dominance in female beef cattle. *Animal Behaviour* 86: 1315-1323.
- Schmidt-Nielsen, K. 1984. *Scaling: Why is Animal Size So Important*. Cambridge University Press, New York, NY, USA.
- Schulte-Hostedde, A. I., and J. S. Millar. 2002. ‘Little chipmunk’ syndrome? Male body size and dominance in captive yellow-pine chipmunks (*Tamias amoenus*). *Ethology* 108: 127-137.
- Sergio, F., J. Blas, and F. Hiraldo. 2009a. Predictors of floater status in a long-lived bird: a cross-sectional and longitudinal test of hypotheses. *Journal of Animal Ecology* 78: 109-118.
- Sergio, F., J. Blas, R. Baos, M. G. Forero, J. A. Donazar, and F. Hiraldo. 2009b. Short- and long-term consequences of individual and territory quality in a long-lived bird. *Oecologia* 160: 507-514.
- Serrano-Meneses, M.A., A. Córdoba-Aguilar, V. Méndez, S. J. Layen, and T. Székely. 2007. Sexual size dimorphism in the American rubyspot: male body size predicts male competition and mating success. *Animal Behaviour* 27: 987-997.
- Sillett, T. S., R. Chandler, A. Royle, M. Kery, and S. A. Morrison. 2012. Hierarchical distance-sampling models to estimate population size and habitat-specific abundance of an island endemic. *Ecological Applications* 22: 1997-2006.
- Sondaar, P. Y. 1986. The island sweepstakes – Why did pygmy elephants, dwarf deer, and large mice once populate the Mediterranean? *Natural History* 95: 50-57.
- Stamps, J. A. and V. V. Krishnan. 1994. Territory acquisition in lizards: I. First encounters. *Animal Behavior* 47: 1375-1385.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, London, England.

Sweitzer, R. A. 1996. Predation or starvation: consequences of foraging decisions by porcupines (*Erethison dorsatum*). *Journal of Mammalogy* 77: 1068-1077.

Swierk, L., M. Ridgway, T. and Langkilde. 2012. Female lizards discriminate between potential reproductive partners using multiple male traits when territory cues are absent. *Behavioral Ecology and Sociobiology* 66: 1033-1043.

Thompson, D. W. 1917. *On Growth and Form*. Cambridge University Press, New York, NY, USA.

Tobler, M. and H. G. Smith. 2004. Specific floater home ranges and prospective behaviour in the European starling, *Sturnus vulgaris*. *Naturwissenschaften* 91: 85-89.

Townsend, A. K., R. Bowman, J. W. Fitzpatrick, M. Dent, and I. J. Lovette. 2011. Genetic monogamy across variable demographic landscapes in cooperatively breeding Florida Scrub-Jays. *Behavioral Ecology* 22: 464-470.

Trivers, R. L. 1972. Parental investment and sexual selection. In *Sexual Selection and the Descent of Man, 1871-1971*. (B. Campbell Editor) Aldine, Chicago, IL, USA. pp. 136-179.

Ursprung, E., M. Ringler, R. Jehle, and W. Hödl. 2011. Strong male/male competition allows for nonchoosy females: high levels of polygynandry in a territorial frog with parental care. *Molecular Ecology* 20: 1759-1771.

Van Valen, L. 1973. A new evolutionary law. *Evolutionary Theory* 1: 1-33.

Wauters, L. A., and A. A. Dhondt. Lifetime reproductive success and its correlates in female Eurasian red squirrels. *Oikos* 72: 402-410.

Weatherhead, P. J. and P. T. Boag. 1995. Pair and extra-pair mating success relative to male quality in red-winged blackbirds. *Behavioral Ecology and Sociobiology* 37: 81-91.

Webster, M. S., S. Pruett-Jones, D. F. Westneat, and S. J. Arnold. 1995. Measuring the effects of pairing success, extra-pair copulations, and mate quality on the opportunity for sexual selection. *Evolution* 49: 1147-1157.

Western Regional Climate Center 2008-2013. Desert Research Institute, Reno, Nevada.
www.wrcc.dri.edu/channel_isl/

Westneat, D. F., P. W. Sherman, and M. L. Morton. 1990. The ecology and evolution of extra-pair copulations in birds. *Current Ornithology* 7: 331-369.

Weigmann, D. D. and T. Nguyen. 2006. Mating system and demographic constraints on the opportunity for sexual selection. *Theoretical Population Biology* 69: 34-47.

Woolfenden, G. E. and J. W. Fitzpatrick. 1996. Florida Scrub-Jay (*Aphelocoma coerulescens*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online:
<http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/228>

Yeaton, R. I. 1974. An ecological analysis of chaparral and pine forest bird communities on Santa Cruz Island and mainland California. *Ecology* 55: 959-973.

Zack, S. and B. J. Stutchbury. 1992. Delayed breeding in avian social systems: the role of territory quality and “floater” tactics. *Behaviour* 123: 194-219.

APPENDIX: dominance interactions

Methods

In order to test for an advantage of large body size in dominance interactions we collected behavioral data during the fall of 2012 and spring of 2013 on 20 radio-tagged yearling Island Scrub-Jays. A five-minute observation period began once a tagged bird had been located and sighted. During those five minutes we recorded whether the focal bird was dominant or subordinate in interactions (Table 2). If a target bird could not be followed for the complete five minutes we recorded how long it was in sight, in seconds, as a measure of our sampling effort.

We calculated two indices of dominance for each Island Scrub-Jay: 1) the absolute number of interactions in which the individual was dominant per unit time sampled; and 2) the ratio of the number of interactions in which the individual was dominant to the number of interactions in which it was subordinate per unit time sampled. We used linear regression to determine whether tarsus length measured in the fall of the first year of life predicted either of the two dominance indices. We separated regression analyses by sex in order to account for sexual size dimorphism in the Island Scrub-Jay (Pitelka 1951).

We also made direct comparisons of the body sizes of dominant and subordinate individuals that participated in paired agonistic interactions. We observed 42 agonistic interactions between first-year radio-tagged jays and other banded jays during the fall of 2012 and the spring of 2013. Due to sexual size dimorphism (Pitelka 1951) we eliminated interactions involving individuals of unknown sex, and pairs of individuals of different sexes. We also eliminated interactions between first-year radio-tagged jays and known territory holders, since experience and territoriality may also influence dominance (Murie & Harris 1978; Holmes *et al.* 1996; Rosell *et al.* 2008). When a given bird dominated the same individual multiple times, we

only included that pair once in the analysis. We also excluded pairs that interacted twice if their status as dominant or subordinate switched between the two interactions. This left a total of six interactions for which we used a paired t-test to compare the tarsus length of radio-tagged males to other non-territorial, or unknown territory status males, not controlling for age. Second, we compared the tarsus length of radio-tagged males to other non-territorial or unknown territory status males of the same age ($n = 4$ interactions). The small sample size prevented statistical comparisons, but we present a summary of the findings. Because we only observed one interaction between first-year females of non-territorial status we were unable to make statistical inferences, and instead present a summary of this interaction.

Results

Tarsus size did not predict the number of interactions per unit time where a first-year Island Scrub-Jay, male or female, was dominant, nor did it predict the ratio of dominant to subordinate interactions per unit time (Table 3). Not controlling for age, dominant males of non-territorial or unknown territory status did not have larger tarsi than subordinate males in agonistic interactions ($t = 1.20$, $df = 5$, $P > 0.1$; Figure 3). In two of the four interactions between non-territorial, first-year male jays, the dominant individual had a larger tarsus, and in the other two interactions the subordinate individual had a larger tarsus (Table 4). We only observed one interaction between first-year, female, non-territorial jays. The dominant and subordinate females in this case had nearly the same tarsus length (45.18 and 45.08 mm respectively, which is within the range of error between repeated measurements on the same individual).

Discussion

In addition to influencing territory acquisition and extra-pair paternity, we expected body size of first-year Island Scrub-Jays would be positively correlated with dominance during social interactions. Contrary to our prediction, we found that body size did not predict the outcome of social interactions with other jays. However, the social interactions we observed of these first-year jays were not restricted to members of the same age class and instead included many interactions with older jays, including territory holders. Body size effects may have been more evident if we had observed a larger sample of interactions with other first-year jays of the same experience and territorial status, since both of these can influence dominance (Murie & Harris 1978; Holmes *et al.* 1996; Rosell *et al.* 2008). Further, in cases where size differences between opponents are small, size may not be a good predictor of outcome (Reichert 1978).

Further study of dominance interactions in first-year Island Scrub-Jays are needed to thoroughly evaluate the role of body size as it relates to dominance in young birds. This could be accomplished by further observational study of dominance interactions of radio-tagged individuals in future field seasons, or an experimental staged dominance trial, such as at a feeding platform.

TABLES

Table 2: Agonistic behaviors recorded during a standardized, 5-minute observation period and their definitions.

Behavior	Dominant/ Subordinate	Definition
Displaced by	Subordinate	Conspecific supplants the focal bird on a perch.
Displaces	Dominant	The focal bird supplants a conspecific on a perch.
Chased by	Subordinate	Conspecific chases the focal bird.
Chases	Dominant	The focal bird is chased by a conspecific.

Table 3: Summary of results for the regression of dominance on tarsus size for both male and female first-year Island Scrub-Jays. # dom is the number of interactions where a focal bird was dominant, #sub is the number of interactions where a focal bird was subordinate, time is the total observation time for a focal bird.

	# dom/ time	(#dom/ #sub)/ time
Males	$R^2 = 0.20, P = 0.11, DF = 13$	$R^2 = 0.11, P = 0.25, DF = 13$
Females	$R^2 = 0.40, P = 0.18, DF = 5$	$R^2 = 0.29, P = 0.27, DF = 5$

Table 4: Summary of agonistic interactions between non-territorial, first-year, male Island Scrub-Jays.

Dominant tarsus (mm)	Subordinate tarsus (mm)	Is dominant larger?
46.95	46.47	Yes
46.99	45.98	Yes
43.69	46.83	No
46.95	48.02	No

FIGURES

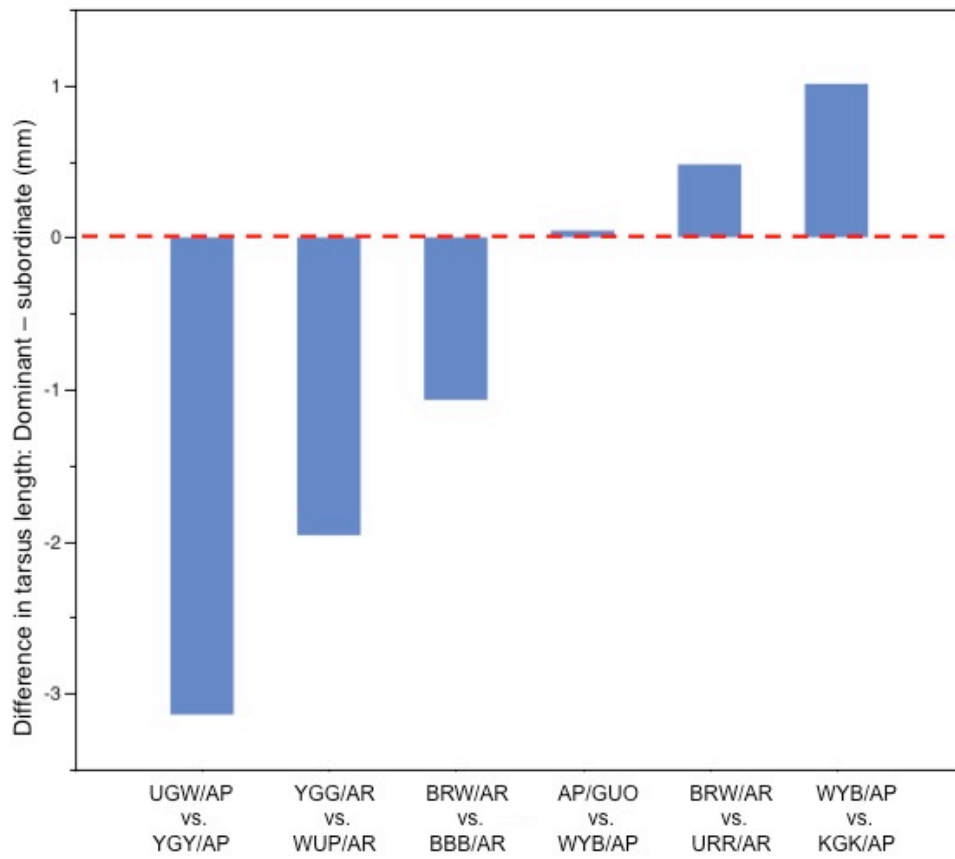


Figure 3: A paired comparison of the tarsus lengths of dominant and subordinate males in agonistic interactions (n = 6). Males compared are not necessarily of the same age, and are of non-territorial, or unknown territorial status.

APPENDIX REFERENCES

Holmes, R. T., P. P. Marra, and T. W. Sherry. 1996. Habitat-specific breeding demography of Black-throated Blue Warblers (*Dendroica caerulescens*): implications for population dynamics. *Journal of Animal Ecology* 65: 183-195.

Murie, J. O., and M. A. Harris. 1978. Territoriality and dominance in male Columbian ground squirrels (*Spermophilus columbianus*). *Canadian Journal of Zoology* 56: 2402-2412.

Pitelka, F. A. 1951. Speciation and ecological distribution of American jays of the genus *Aphelocoma*. *University of California Publications in Zoology* 50: 195-464.

Riechert, S. E. 1978. Games spiders play: behavioral variability in territorial disputes. *Behavioural Ecology and Sociobiology* 3: 135-162.

Rosell, F., G. Gundersen, and J. F. Le Galliard. 2008. Territory ownership and familiarity status affect how much male root voles (*Microtus oeconomus*) invest in territory defense. *Behavioral Ecology and Sociobiology* 62: 1559-1568.