

RESEARCH ARTICLE

Body size is associated with yearling breeding and extra-pair mating in the Island Scrub-Jay

Michelle A. Desrosiers,^{1,*} Kathryn M. Langin,^{1,2} W. Chris Funk,^{1,2} T. Scott Sillett,³ Scott A. Morrison,⁴ Cameron K. Ghalambor,^{1,2,5} and Lisa M. Angeloni^{1,2}

¹Department of Biology, Colorado State University, Fort Collins, Colorado, USA

²Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado, USA

³Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, DC, USA

⁴The Nature Conservancy, San Francisco, California, USA

⁵Centre for Biodiversity Dynamics (CBD), Department of Biology, Norwegian University of Science and Technology (NTNU), Trondheim, Norway

*Corresponding author: michelle.desrosiers@gmail.com

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ABSTRACT

Large body size is an important determinant of individual fitness in many animal species, especially in island systems where habitat saturation may result in strong intraspecific competition for mates and breeding territories. Here we show that large body size is associated with benefits to yearling breeding and extra-pair mating in the Island Scrub-Jay (*Aphelocoma insularis*), endemic to Santa Cruz Island, California. This species is ~20% larger than its mainland congener, consistent with the island syndrome, indicating that body size may be a trait under selection. From 2009 to 2013, we quantified the reproductive success of a marked population of Island Scrub-Jays, tracked which yearlings acquired a breeding territory and bred, and measured the occurrence of extra-pair paternity. Two potential contributors to fitness were positively related to body size. Larger yearling males were more likely to breed, possibly due to greater behavioral dominance during aggressive encounters. Larger males were also less likely to lose paternity to extra-pair males and, anecdotally, extra-pair males were larger than the social male cuckolded. This study provides evidence that larger males may have a fitness advantage over smaller males by breeding earlier and avoiding paternity loss, but estimates of lifetime reproductive success are ultimately needed for Island Scrub-Jays and other long-lived species.

Keywords: *Aphelocoma insularis*, body size, California, extra-pair mating, Island Scrub-Jay, island syndrome, Santa Cruz Island, territory acquisition

LAY SUMMARY

- The body size of an animal can influence its ability to pass on its genes.
- In some species larger individuals may be better able to secure a place to breed, and larger males may father a greater proportion of offspring in their nest.
- We examined whether body size is related to territory acquisition, breeding, and offspring parentage in the Island Scrub-Jay, a species that is restricted to Santa Cruz Island, California, and is larger than its sibling species on the nearby mainland.
- Yearling jays that were larger in body size were more likely to acquire a territory and breed, and larger males of any age were less likely to lose paternity to extra-pair matings.
- These results suggest that larger Island Scrub-Jays have greater reproductive success.

El tamaño del cuerpo está asociado con la reproducción de la cría de un año y el apareamiento extra-pareja en *Aphelocoma insularis*

RESUMEN

El tamaño corporal grande es un determinante importante de la aptitud biológica individual en muchas especies animales, especialmente en sistemas insulares donde la saturación del hábitat puede resultar en una fuerte competencia intraespecífica por parejas y territorios de reproducción. Aquí mostramos que el tamaño corporal grande se asocia

con beneficios para la reproducción de la cría de un año y el apareamiento extra-pareja en *Aphelocoma insularis*, un ave endémica de la Isla Santa Cruz, California. Esta especie es ~20% más grande que su congénere continental, lo que concuerda con el síndrome de la isla, lo que indica que el tamaño corporal puede ser un rasgo bajo selección. De 2009 a 2013, cuantificamos el éxito reproductivo de una población marcada de *A. insularis*, rastreamos qué crías de un año adquirieron un territorio de reproducción y se reprodujeron, y medimos la ocurrencia de paternidad extra-pareja. Dos contribuyentes potenciales a la aptitud biológica se relacionaron positivamente con el tamaño corporal. Los machos de un año más grandes tuvieron más probabilidades de reproducirse, posiblemente debido a un comportamiento dominante más fuerte durante los encuentros agresivos. Los machos de un año más grandes también fueron menos propensos a perder la paternidad frente a los machos extra-pareja y, anécdoticamente, los machos extra-pareja fueron más grandes que el macho social objeto de infidelidad. Este estudio proporciona evidencia de que los machos más grandes pueden tener una ventaja de aptitud biológica sobre los machos más pequeños al reproducirse antes y evitar la pérdida de la paternidad, pero las estimaciones del éxito reproductivo a lo largo de toda la vida son finalmente necesarias para *A. insularis* y otras especies longevas.

Palabras clave: adquisición de territorio, apareamiento extra-pareja, *Aphelocoma insularis*, California, Isla Santa Cruz, síndrome de la isla, tamaño corporal

INTRODUCTION

An organism's body size fundamentally shapes all aspects of its biology (Peters 1983, Calder 1984, Schmidt-Nielsen 1984, Bonner 2006). Factors correlated with body size across taxa may include physiological and metabolic rates (Bouteiller-Reuter and Perrin 2005, Bonner 2006), predator avoidance or defense (Christensen 1996, De Robertis et al. 2000, Arendt 2009, Geary et al. 2012), locomotor performance (Dial 2003), timing and investment of energy in reproduction (Roff 1992, Stearns 1992), and mate choice (Andersson 1994). These factors and their interactions can shape selection pressures favoring smaller or larger body sizes (Peters 1983, Calder 1984, Schmidt-Nielsen 1984).

Advantages of a large body size have been best documented in animals that exhibit sexual size dimorphism, where individuals of 1 sex, often males, are larger and use their size to compete for breeding opportunities (Andersson 1994). In such cases, large body size often confers dominance in social hierarchies (Eckert and Weatherhead 1987a, Funghi et al. 2015) and has been implicated in territory acquisition across a variety of taxa (Mathis 1990, Mazerolle and Hobson 2002, Jenssen et al. 2005, Serrano-Meneses et al. 2007, Iossa et al. 2008, Natsumeda et al. 2011). However, a positive relationship between body size, dominance, and territory acquisition is not universal, and in some cases, a smaller body size may even be associated with dominance, due to greater locomotor ability and maneuverability in contests (Schulte-Hostedde and Millar 2002, Martin and Ghalambor 2014). Further, age and experience can trump body size in dominance and territory acquisition (Shutler and Weatherhead 1991, Berdoy et al. 1995, Sergio et al. 2009a, Šárová et al. 2013). Body size also has the potential to positively influence reproductive success, particularly when used in male–male competition or as an indicator of quality during mate choice (Searcy 1979, Yasukawa 1981, Andersson 1994, Griffith et al. 2002, Swierk et al. 2012). Even in socially

monogamous species, which are expected to have reduced sexual selection for male body size as compared to polygynous species (Dunn et al. 2001, Weigmann and Nguyen 2006), larger males may retain a fitness advantage through extra-pair matings (i.e. copulations outside of the territorial pair bond; Griffith et al. 2002, Schlicht et al. 2015, Wells et al. 2015). However, in some species, body size appears unimportant, and other traits, such as plumage variation, are better indicators of extra-pair mating success (Yezerinac and Weatherhead 1997, Johnsen et al. 2001, Balenger et al. 2009, Cramer et al. 2017).

Advantages of a larger body size may be particularly pronounced in island systems. Breeding territories may be limited on islands because of habitat saturation (Komdeur 1992), resulting in a large, nonbreeding portion of the population, where some individuals never gain the opportunity to breed (Newton 1994, Buston and Cant 2006, Kingma et al. 2016). Thus, competition for breeding territories 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 and Cant 2006). It is unclear if large body size remains advantageous in gaining or preventing extra-pair paternity in island populations, where population densities are higher and thus where extra-pair matings may be more common (Griffith et al. 2002, Maldonado-Chaparro et al. 2018; but see Conrad et al. 2001).

Here we assess the degree to which body size impacts territory acquisition and patterns of extra-pair paternity in the Island Scrub-Jay (*Aphelocoma insularis*), a species that is endemic to Santa Cruz Island, California. Island Scrub-Jays are ~20% larger than their mainland congeners (Pitelka 1951), indicating that body size may be a trait under selection in this insular population. Individuals typically do not acquire a territory until a median age of 4 years and thus spend their early years as nonbreeders (Atwood 1980a, Collins and Corey 1994). In contrast, California Scrub-Jays (*A. californica*) and Florida Scrub-Jays (*A. coerulescens*)

tend to acquire territories after 1 and 2 years, respectively (Woolfenden and Fitzpatrick 1996, Carmen 2004). The late transition to territory holding and thus to breeding in the Island Scrub-Jay means a proportion of the population are sexually mature but nonbreeding individuals (Curry and Semple Delaney 2002). Unlike Florida Scrub-Jays, Island Scrub-Jays do not cooperatively breed (Atwood 1980b, Collins and Corey 1994, Delaney 2003, personal observation). Once individuals acquire a territory, mated pairs are socially monogamous and jointly defend a multi-purpose territory year-round, potentially for life (Atwood 1980a, Curry and Semple Delaney 2002).

Given the potential for strong competition among Island Scrub-Jays for breeding territories, we hypothesized that body size is an important determinant of competitive ability and individual quality. We predicted that larger yearling Island Scrub-Jays (of either sex) would be more likely to acquire a breeding territory and breed. We also predicted that male Island Scrub-Jays that fathered extra-pair offspring would be larger than the social mates they cuckolded and larger jays would be less likely to lose paternity due to extra-pair matings. To test these predictions, we quantified the reproductive success of a marked population of Island Scrub-Jays, tracking which birds acquired a breeding territory and bred as yearlings and the occurrence of extra-pair paternity in the population.

METHODS

Study System and General Field Methods

Santa Cruz Island is 32 km off the coast of Santa Barbara, California, USA. The 249 km² island has a Mediterranean-type climate characterized by cool, wet winters and hot, dry summers (Junak et al. 1995, Fisher et al. 2009). We worked on 3 study sites of 115, 163, and 226 ha in area. These plots were located in oak chaparral habitat that occurred as a gradient from continuous canopy to a grassland mosaic (see Caldwell et al. 2013).

We captured Island Scrub-Jays during spring (February through June) and fall (September through December) field seasons in 2009 through 2012 to collect morphological measurements. We trapped birds using drop box traps and mist nets baited with peanuts. We marked jays with a unique combination of up to 4 colored plastic leg bands and 1 numbered U.S. Geological Survey band. We measured tarsus length at least 2 times, sometimes 3, per capture of each individual, and the average of these measures was used in analyses. The intra-class correlation coefficient (r) of repeat tarsus measurements used in this study as calculated with the *ICCbare* function in package *ICC* 2.3.0 was 0.89. We used tarsus length as an index of body size (Rising and Somers 1989, Freeman and Jackson 1990) because, unlike other potential measurements,

including body mass, bill length (Davis 1954), and tail length, tarsus length does not vary seasonally or with age, and our measurements of different individuals were taken across multiple months or even years. The tarsus of 150 jays of all ages captured in a 2-month span when not molting was positively correlated with body mass ($r = 0.77$, $P < 0.001$), wing length ($r = 0.55$, $P < 0.001$), tail length ($r = 0.53$, $P < 0.001$), and length between nares and bill tip ($r = 0.51$, $P < 0.001$, only after hatch-year birds). We also collected 70–100 μ L 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. Molecular sexing methods are described in Langin et al. (2015).

During the breeding season (mid-February to late June) of 2010, 2011, and 2012, we monitored all established breeding pairs on each of our 3 study plots and attempted to find all nesting attempts to sample young for paternity analysis (2010: 20, 15, and 22 pairs; 2011: 21, 19, and 27 pairs; 2012: 23, 21, and 26 pairs). Territories of monitored pairs represent complete coverage of the study plots. We collected 50–100 μ L of blood from nestlings in all accessible nests 11 to 13 days after hatching, including some ($n = 17$) that were accessed with a step ladder or by climbing trees. Some nests ($n = 31$) were inaccessible, typically due to the height and/or strength of the substrate, but we do not believe this resulted in sampling bias, given we were able to sample widely across breeding pairs of varying ages and experience. Thirty-two breeding pairs were sampled once, hence contributing a single brood to our dataset. Six breeding pairs were sampled twice; 5 of these pairs had 2 broods sampled across different years, and 1 pair had 2 broods sampled within the same year (due to nest failure and subsequent re-nesting). Three breeding pairs were sampled 3 times, with 2 broods in the same season and 1 in another.

Yearling Pair Formation, Territory Acquisition, and Breeding

Although Island Scrub-Jays typically defer breeding for multiple years, some yearlings form pair bonds, defend breeding territories, and attempt breeding. To describe patterns of pair bond formation and breeding status of yearling jays, we fit 40 hatch-year individuals with Lotek Pip Ag radio transmitters ($\leq 3\%$ of body mass) over 2 years: 2011 and 2012; individuals outfitted with transmitters each year were the first 20 hatch-year birds caught in October. Transmitters were attached with leg-loop harnesses (Bowman and Aborn 2001) made of elastic thread designed to degrade and fall off birds within 12 months.

We aimed to collect a point location confirmed by visual identification on each radio-tagged jay each time we visited its plot, which occurred every 1–4 days, depending on weather and personnel (average time between observations:

mean $\pm$ SD = 2.71 days $\pm$ 2.32). After confirmation, we observed jays for a minimum of 5 min 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). Jays captured in fall 2011 were followed from the second week of February through the third week of May in 2012; those captured in fall 2012 were tracked from the second week of March through the second week of May in 2013. Breeding activity slows and new nesting attempts typically cease in late May, with earlier cessation in drier years.

We classified a jay as being paired if we observed it engaging in pair behaviors with the same individual consistently throughout at least half of the breeding season. A paired jay was not classified as a territorial breeder until we documented a complete nesting attempt (i.e. nest-building, egg-laying, and nest attendance). Jays classified as territorial breeders included radio-tagged individuals that bred in 2012 and 2013, as well as non-radio-tagged individuals banded as hatch-years in 2009–2012 that bred as yearlings during a subsequent nesting study. Breeding as a yearling is a relatively rare event; therefore, we included these non-radio-tagged breeders in our analysis to increase our power to detect a pattern. The only jays classified as nonbreeders in our analysis were those that were radio-tagged, were followed for the duration of their yearling spring, and were not observed to nest. We were able to confidently assign breeding status (i.e. nonbreeder, paired, attempted territory holder, territorial breeder) to 27 out of 40 radio-tagged jays due to the frequency with which we tracked them and checked any nests built. Of the remaining 13 radio-tagged jays, 7 appeared to be depredated prior to their first potential breeding season (1 in fall 2011, 6 over the winter of 2012–2013), as their transmitters were found with piles of plucked or bitten feathers and body parts, including leg bands; 3 dropped their transmitters prior to their first spring; 2 transmitters had failed batteries (the birds were re-sighted with their transmitter attached, but no signal could be detected); and 1 was never detected, either due to battery failure or movement of the jay out of range of the study plots.

Measurement of Extra-Pair Paternity

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 (AIAAGG13, ApCo2, PJGATA3, PJAAAG9, PJGATA2, CmAAAG30, CmAAAG11, CmAAAG25, CmAAAG6). We amplified microsatellites and scored electropherograms as described in [Langin et al. \(2015\)](#).

We used CERVUS 3.0.7 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 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 territorial females of sampled broods were genetic mothers, as no evidence of conspecific brood parasitism has been found in the species ([Delaney 2003](#)). With the 9 variable microsatellite loci used, the median probability that an unrelated parent could not be excluded when only the offspring genotype was known was 1.2×10^{-3} , the probability that an unrelated candidate male could not be excluded when the offspring and maternal genotype was specified was 3.7×10^{-5} , and the probability of not excluding an unrelated parent pair given only the genotype of the offspring was 2.0×10^{-8} . 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](#)).

We tested for evidence of extra-pair mating using samples from 156 offspring from 52 broods (clutch size: 3.67 ± 0.09 , range: 1–5 eggs) that were produced by 41 pairs. We had maternal genotypes for 50 of the 52 broods, and 39 of the 41 pairs. Candidate fathers ($n = 184$ over the entire study) included all males and individuals of unknown sex 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 first potential breeding season, territorial jays typically stay on the same territory for life, and plots were not immediately adjacent to each other ([Atwood 1980b](#), [Caldwell et al. 2013](#)). We separated our paternity analyses by year to exclude full siblings from the same nest and individuals not re-sighted in or after that season (i.e. presumed dead) from our list of candidate fathers. We rejected 1 assignment of paternity to a full sibling from a previous year in favor of the social male who was the only other male identified with a similar, positive LOD score; this full sibling held a territory ~750 m (and 4 territories) away, making it unlikely to be the father, given the high fidelity of Island Scrub-Jays to their territories during the breeding season ([Atwood 1980b](#), personal observation). CERVUS required the input of an estimated number of candidate males per plot, a value that is meant to incorporate sampled as well as un-sampled sires. We needed to develop plot-specific estimates that accounted for all sampled and un-sampled territorial and non-territorial males of breeding age, not simply males we had a record of in our breeding ecology study. To do this,

we used the area of each plot from Caldwell et al. (2013), and estimated habitat-specific densities from Sillett et al. (2012), divided by 2 ($n = 32, 63$, and 46 estimated candidate males). We conservatively set the percentage of males sampled at 80%, and the typing error rate to 0.01 after we had re-typed 8% of the individuals sampled in the genetic dataset, from amplification to allele scoring, and found no mismatches. We assigned paternity at CERVUS's 95% confidence cutoff.

Body Size Comparisons

We used R 4.0.2 (R Core Team 2020) for all analyses of body size. We used logistic regression to assess if body size predicted whether or not a yearling acquired a territory and bred, and if body size predicted whether or not a male lost paternity to extra-pair matings (i.e. if there was evidence of extra-pair paternity across any of his sampled eggs and clutches). Yearling territory acquisition analyses were separated by sex. Males included in the paternity-body size analysis were a subset of those evaluated in paternity assignment. Fourteen total males were classified as potentially uncuckolded. We restricted our sample to males that had at least 1 brood that was completely sampled (i.e. where the number of nestlings sampled and scored was equal to the known number of eggs laid) to reduce the possibility of including cases with undetected cuckoldry. Three of these 14 uncuckolded males had offspring sampled from multiple broods, at least one of which was completely sampled, with no evidence of paternity loss in any brood. A male was classified as cuckolded if extra-pair offspring were detected in any of his sampled broods. One cuckolded male was excluded from the analysis because we did not measure his tarsus length, leaving 5 cuckolded males (2 males with 1 sampled brood and 3 males with more than 1 sampled brood). For all regressions, we calculated McFadden's pseudo R^2 and likelihood-ratio P -values based on the chi-squared distribution. The likelihood-ratio P -value calculation performs best when sample sizes are small as in our analyses (Agresti 2007; $n = 12$ female yearling breeders, $n = 9$ female yearling nonbreeders, $n = 15$ male yearling breeders, $n = 16$ male yearling nonbreeders, $n = 5$ cuckolded social males, and $n = 14$ uncuckolded social males). In all of our statistical tests, we considered results significant at the $\alpha = 0.05$ level.

RESULTS

Yearling Pair Formation, Territory Acquisition, and Breeding

Larger male Island Scrub-Jays were more likely to acquire a territory and breed as yearlings ($r^2 = 0.12$, $P = 0.02$), but larger female Island Scrub-Jays were not ($r^2 = 0.02$, $P = 0.46$; Figure 1). Of 27 yearling jays that were radio-tagged and

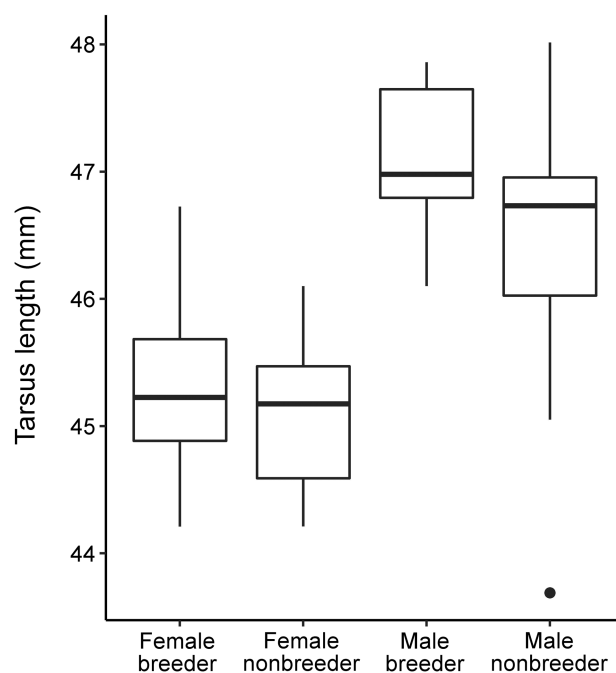


FIGURE 1. Tarsus length of male and female Island Scrub-Jays that acquired a territory and bred as yearlings compared to those that did not (males: $n = 15$ breeders and $n = 16$ nonbreeders; females: $n = 12$ breeders and $n = 9$ nonbreeders).

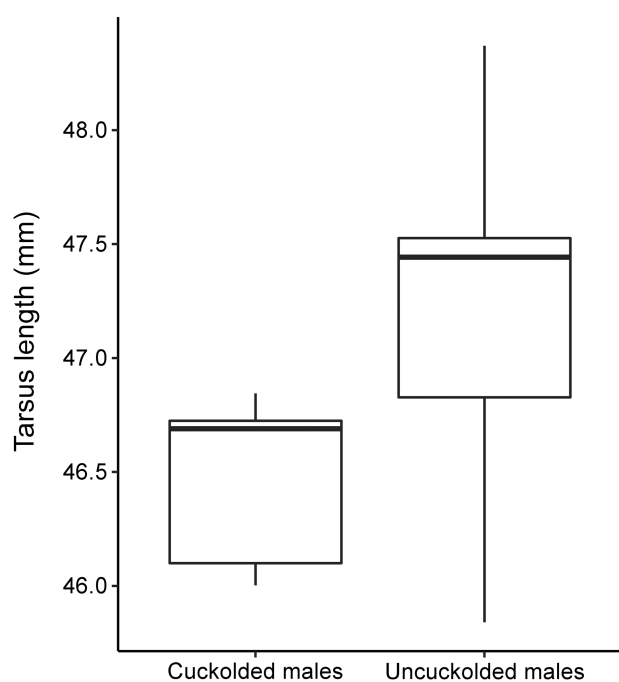
tracked throughout their first potential breeding season, 11 engaged in some form of reproductive behavior. Two males successfully defended a small territory, built a nest, and bred. The remaining 9 individuals (8 males, 1 female) formed pairs but did not breed. Seven of these (6 males, 1 female) defended a small territory for part of the season but were unable to maintain it; the other 2, both male, were unable to establish and defend a territory. The remaining 16 jays (8 males, 8 females) were never observed engaging in reproductive behavior, but were often detected 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 3 occasions over fewer than 9 days) and therefore not indicative of long-term pair bonding.

Extra-Pair Paternity

We were able to assign a sire to 143 of 156 offspring. Assignments and offspring excluded from the further analysis are summarized in Table 1. Twelve nestlings (8%) were identified as extra-pair offspring, including 6 for which no male was assigned, even though the social male was included in the candidate father file. Six pairs (15%) had a brood that contained at least 1 extra-pair offspring. The percentage of extra-pair offspring within these broods ranged from 25% to 100%. We were able to assign paternity to a specific extra-pair male in 4 broods that contained extra-pair young. One extra-pair male was identified as

TABLE 1. Breakdown of paternity assignments by offspring. SM is social male, EPM is extra-pair male.

Assignment and confidence	Number of offspring	Additional information
SM 95%—no others with positive scores	95	
SM 95%—one other with positive score	35	
SM 95%—two others with positive score	4	For one of these offspring, the female was not sampled.
SM 95%—three others with positive score	1	The female was not sampled.
EPM 95%—no others with positive scores	4	
EPM 95%—SM with positive LOD score	2	In both cases the female was sampled, offspring were typed at 8 and 9 out of 9 loci, and LOD scores of EPM and SM were not similar.
No male assigned	6	Assumed to be extra-pair young since SM was in candidate list and not assigned.
SM after the rejection of original assignment	1	Paternity assigned to full sibling that was a territory holder ~750 m away. SM was the only other identified male with similar, positive LOD score.
Excluded from further consideration	7	Nestlings were typed at 6 or less loci, the female was not sampled in 1 case, and similar, positive LOD scores were assigned to multiple males.

**FIGURE 2.** Tarsus length of male Island Scrub-Jays that were cuckolded compared to those that were not ($n = 5$ cuckolded males, $n = 14$ uncuckolded males).

the sire in cases of multiple extra-pair young in a single brood. Three of the extra-pair sires were neighboring territory holders; the territory status of the other sire was unknown. We found that smaller males were more likely to be cuckolded than larger males ($r^2 = 0.26$, $P = 0.02$; Figure 2), and that the cuckolding male was larger than the social male in 2 out of 3 cases where we had tarsus measurements.

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 (Andersson 1994, Robertson 1996, Piper et al. 1999). We found that 2 potential contributors to fitness—the ability to acquire a territory and breed during an individual's first year and avoidance of paternity loss due to extra-pair matings—were positively related to body size in the Island Scrub-Jay. We found larger body size is associated with the ability of yearling jays to breed (Figure 1), possibly due to greater behavioral dominance during aggressive encounters (Martin and Ghalambor 2014). We also found that larger males were less likely to lose paternity to extra-pair males (Figure 2) and some anecdotal evidence that extra-pair males were larger than the social mate cuckolded (in 2 out of 3 cases), consistent with previous literature suggesting that body size can provide a mating advantage to males, even in socially monogamous species, where extra-pair matings have the potential to skew reproductive success (Dunn et al. 2001, Schlicht et al. 2015, Wells et al. 2015, Brouwer and Griffith 2019). Below, we discuss these results in more detail and within the context of this island system.

Body Size and Yearling Breeding

Island Scrub-Jays, which are physiologically capable of reproducing in their first year following hatching (Atwood 1980b, Caldwell et al. 2013), exhibited a wide range of reproductive behaviors. Many first-year individuals did not

engage in any breeding behavior, some formed a pair bond and attempted to jointly defend a small territory, and a few built nests and produced eggs. Formation of breeding pair relationships prior to territory acquisition has been noted in other bird species (e.g., Eurasian Oystercatcher [*Haematopus ostralegus*]; Heg et al. 2000). The gradient of breeding behavior we observed in the Island Scrub-Jay is similar to that observed in young Western Scrub-Jays (Carmen 2004) but differs from the cooperative breeding system of other *Aphelocoma*, where young will forego their own reproduction and stay on their natal territory to help raise siblings (Woolfenden and Fitzpatrick 1984, Burt and Peterson 1993). Helping and other forms of cooperative breeding have never been observed in Island Scrub-Jays (Atwood 1980b, Collins and Corey 1994, Delaney 2003, personal observation).

Nonbreeding birds employ a wide range of behavioral strategies to either gain a breeding vacancy or establish non-territorial social dominance, which may contribute to later territory acquisition. One observed strategy of nonbreeding birds is to spend time on territories of breeding individuals, either waiting for a vacancy or attempting to evict an owner (Zack and Stutchbury 1992, Tobler and Smith 2004). This pattern is especially prevalent in long-lived species that hold year-round territories in saturated habitat (e.g., tropical species) or species that migrate with high site fidelity (Zack and Stutchbury 1992, Duca and Marini 2014). Yearling Island Scrub-Jays that acquired a territory and bred often did so on the borders of established territories, and home ranges for nonbreeding yearlings typically overlapped multiple established territories (personal observation), suggesting that they spent time prospecting near established pairs. Breeding vacancies, which occur when a member of an established pair dies, are filled quickly in the Island Scrub-Jay, often within days, favoring individuals familiar with the area (Collins and Corey 2005, Mudry 2008, personal observation).

A positive relationship between body size and the acquisition of a breeding territory has been noted in many taxa (e.g., Andersson 1994, Marra and Holmes 2001, Iossa et al. 2008). Although body size is correlated with age and experience in many species (Arcese 1987, Berdoy et al. 1995, Côté 2000, Hyman et al. 2004, Kiyota 2005), age was not a confounding variable in our study of early breeding. Thus, our study supports the idea that body size can confer an advantage when there is competition for territories caused by limited breeding vacancies and a nonbreeding portion of the population. The early acquisition of a territory and opportunity to breed may be important to the ultimate fitness of an individual, as early breeding provides more opportunities to produce young and gain valuable experience that can translate to greater lifetime reproductive success (Ainley et al. 1983, Forslund and Pärt 1995). However, in some species, a larger body size is associated

with shortened life span (Ringsby et al. 2015), and early breeding is associated with reduced reproductive performance later in life (Reed et al. 2008), although the latter is not observed in the closely related Florida Scrub-Jay (Wilcoxon et al. 2010).

The role of body size in reproductive success of the Island Scrub-Jay deserves further inquiry. Future studies could determine whether body size influences the quality of the territory acquired (Eckert and Weatherhead 1987b, Holmes et al. 1996, Sergio et al. 2009b) by looking at ecological factors such as predation risk and the availability of good nest sites. Territories with greater vegetation height and complexity allow for better nest concealment (Caldwell et al. 2013). Additionally, larger individuals may defend their nest against predators more aggressively (Larsen et al. 1996), may be able to invest greater amounts of energy in the production of larger offspring (Boltnev and York 2001), or if they live longer, may have more opportunities to reproduce (Weatherhead and Boag 1995).

Body Size and Extra-Pair Paternity

Our results suggest that being a large male Island Scrub-Jay contributes to an individual's reproductive success through avoidance of paternity loss to extra-pair matings, and might increase the chance to gain extra-pair matings. The amount of extra-pair paternity we detected in the Island Scrub-Jay (8% of offspring, 15% of breeding pairs) is similar to levels described by Delaney (2003) and is relatively low for a socially monogamous passerine (Brouwer and Griffith 2019). Our estimate falls between those of the Island Scrub-Jay's mainland congeners: the California Scrub-Jay (21% of offspring; Delaney 2003) and the cooperatively breeding Florida Scrub-Jay (0%; Townsend et al. 2011). Multiple factors could explain differences in rates of extra-pair paternity between island and mainland 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, Krokene and Lifjeld 2000, Griffith et al. 2002). Lower extra-pair paternity in the Island Scrub-Jay compared to the California Scrub-Jay is consistent with this hypothesis. However, some island species exhibit greater levels of extra-pair paternity than their mainland counterparts (Fridolfsson et al. 1997), even when genetic diversity is lower in the island population (Charmantier and Blondel 2003), possibly due to the disproportionate influence of high breeding density and resource limitation.

Traditionally, it has been posited that females must acquire benefits to engage in extra-pair matings, especially if they risk losing male parental care (Dixon et al. 1994, Perlut et al. 2012) or exposure to sexually transmitted diseases

(Forstmeier et al. 2014). Benefits can be direct, such as access to resources, or indirect, such as maximizing the genetic diversity or genetic quality of their offspring (Brouwer and Griffith 2019). If body size reflects underlying genetic quality and is heritable, then our results are consistent with the hypothesis that females seek “good genes” for their offspring by mating with larger males (Trivers 1972, Møller 1988, Westneat et al. 1990, Birkhead and Møller 1992). However, recent analyses suggest that extra-pair mating in females may be a nonadaptive byproduct of male behavior, including coercion by large males (Forstmeier et al. 2014, Hsu et al. 2015). Therefore, we cannot rule out the possibility that the patterns we observed were due to large social males who were competitively superior in territory defense or mate guarding (Whittingham and Lefjeld 1995, Currie et al. 1998, Qvarnström et al. 2000).

Body Size and Implications for Fitness

We found a positive relationship between body size and 2 components of fitness, yearling breeding, and extra-pair paternity, suggesting there could be selection for increased body size. Ultimately, such patterns need to be examined in the context of lifetime reproductive success; however, they provide a set of hypotheses for the mechanisms driving the evolution of larger body size in the Island Scrub-Jay relative to their closest relative, the California Scrub-Jay (Pitelka 1951, Costanzo et al. 2017). The Island Scrub-Jay is larger than the California Scrub-Jay (Pitelka 1951), and the 2 species are estimated to have diverged ~1 million years ago (McCormack et al. 2011). Island taxa often differ in body size from their mainland congeners due to a variety of interacting factors, such as reduced emigration, reduced species diversity, changes in competition and predation, and resource limitation (Foster 1964, MacArthur and Wilson 1967, Yeaton 1974, Palkovacs 2003, Lomolino 2005). Indeed, previous explanations for the larger body size of Island Scrub-Jay have invoked reduced interspecific competition due to the simplified avian community on Santa Cruz Island as compared to the mainland (Pitelka 1951, Grant 1965). This reduction in competition among species is thought to open up niches that are not available on the mainland (Grant 1965). Additionally, because population densities are often higher on islands (Yeaton 1974, George 1987, Ricklefs and Lovette 1999), elevated intra-specific competition for limited breeding territories has also been suggested to select for larger body size as a way of obtaining a dominance advantage over smaller individuals (Newton 1994, Robinson-Wolrath and Owens 2003, Buston and Cant 2006). Our results on the role of body size in early territory acquisition and breeding are consistent with this hypothesis. The saturated breeding habitat of Santa Cruz Island (Atwood 1980b, Caldwell et al. 2013, Bakker et al. 2020), the later median age of first breeding

(Atwood 1980a), the relationship between early breeding and body size, and our findings on extra-pair matings suggest several correlated mechanisms favoring the evolution of larger body size in the Island Scrub-Jay.

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