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RESEARCH ARTICLE

Competition and aggression for nest cavities between Striated Pardalotes and endangered Forty-spotted Pardalotes

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ABSTRACT

The Forty-spotted Pardalote (*Pardalotus quadragintus*) is an endangered songbird with specialized habitat requirements, including *Eucalyptus viminalis* trees for foraging and tree cavities for nesting. The species was originally distributed throughout eastern Tasmania, Australia, but habitat loss and fragmentation resulted in the contraction of its range to just 3 islands and several remnant mainland patches, primarily in the southeast of the state. The species' remaining habitat is exclusively second-growth forest, with reduced nest-cavity availability, and it competes for cavities with a common generalist, the Striated Pardalote (*Pardalotus substriatus*). This study documents the frequency of cavity takeover across the major populations of Forty-spotted Pardalotes on Maria Island, Bruny Island, and mainland Tasmania. Additionally, the intensity of interspecific aggression by pardalotes toward conspecific and heterospecific competitors at nest sites was assessed using a model presentation experiment. Striated Pardalotes usurped $\sim$10% of Forty-spotted Pardalote nest sites across all study areas, and up to 17% of cavities within a single region (mainland Tasmania). Conversely, Forty-spotted Pardalotes never usurped Striated Pardalote nests. Most takeovers (79%) occurred during the nest-building stage, although Striated Pardalotes removed or crushed Forty-spotted Pardalote eggs in 21% of takeovers (4 nests). However, there was no change in nest defense aggression across nest stages. Striated Pardalotes displayed equal aggression toward conspecific and heterospecific models, whereas Forty-spotted Pardalotes were more aggressive toward conspecifics. These results show that Striated Pardalotes are the dominant competitor for nest cavities, and reduce the breeding success of Forty-spotted Pardalotes by usurping their nest sites. Nest boxes are a promising option for restoring the availability of nest sites for Forty-spotted Pardalotes, but given the competition from Striated Pardalotes for nest sites, nest-box placement should take advantage of species differences in nest-site selection to minimize conflict.

Keywords: interspecific aggression, competition, cavity-nesting bird, pardalote, nest defense, endangered species, tree cavities, tree hollows

Competencia y agresión por cavidades para anidación entre *Pardalotus striatus* y la especie amenazada *Pardalotus quadragintus*

RESUMEN

Pardalotus quadragintus es un ave amenazada con requerimientos de hábitat especializados, que incluyen árboles de *Eucalyptus viminalis* que proveen alimento y cavidades para anidación. Originalmente la especie estaba distribuida a través del este de Tasmania, Australia, pero la pérdida del hábitat y la fragmentación resultaron en la contracción de su distribución a sólo tres islas y varios parches remanentes en el continente, principalmente en el sureste del estado. El hábitat restante es exclusivamente bosque secundario con disponibilidad reducida de cavidades para la anidación y *P. quadragintus* compite por las cavidades con la especie generalista *P. striatus*. Este estudio documenta la frecuencia de adquisición de cavidades a través de las poblaciones principales de *P. quadragintus* en isla Bruny, isla Maria y la isla principal de Tasmania. Además, se evaluó la intensidad de las agresiones interespecíficas de las dos especies de *Pardalotus* hacia competidores coespecíficos y heteroespecíficos en los sitios de anidación usando un experimento de presentación de modelos. *P. striatus* usurpó 9.7% de los sitios de anidación de *P. quadragintus* a través de las áreas de estudio y hasta 16.7% de las cavidades en una sola región (isla principal de Tasmania). Por el contrario, *P. quadragintus* nunca usurpó los nidos de *P. striatus*. La mayoría de las adquisiciones ocurrieron durante la etapa de construcción de los nidos, aunque *P. striatus* removió o aplastó los huevos de *P. quadragintus* en 21% de las adquisiciones (4 nidos). Sin embargo, no hubo cambio en las agresiones de defensa de los nidos a través de sus etapas. *P. striatus* mostró agresividad similar hacia modelos coespecíficos y heteroespecíficos, mientras que *P. quadragintus* fue más agresivo hacia los coespecíficos. Estos resultados muestran que *P. striatus* es el competidor dominante por las cavidades para anidación y reduce el éxito reproductivo de *P. quadragintus* al usurpar sus sitios de anidación. Los nidos artificiales son una opción prometedora para restaurar la disponibilidad de sitios de anidación para *P. quadragintus*, pero dada la

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competencia con *P. striatus* por los sitios de anidación, la ubicación de los nidos debería tener en cuenta las diferencias entre ambas especies en la selección de los sitios de anidación para minimizar el conflicto.

Palabras clave: agresión interespecífica, ave anidante de cavidades, cavidades en árboles, competencia, defensa del nido, especie amenazada, huecos en árboles.

INTRODUCTION

The Forty-spotted Pardalote (*Pardalotus quadragintus*) is an endangered songbird found in forests and woodlands of eastern Tasmania, Australia, where it is currently experiencing unexplained decline within existing habitat. These birds are specialists of *Eucalyptus viminalis* (white gum trees). They rely strongly on manna, a sugary exudate of *E. viminalis* foliage, for food. Within *E. viminalis* habitat, they also usually use tree cavities for nesting (Woinarski and Rounsevell 1983). Historically, Forty-spotted Pardalotes were found throughout eastern Tasmania, but their distribution contracted with forest clearing and fragmentation following European settlement. Currently, they are limited to an area <4,500 ha in size, with major populations in southeastern Tasmania on Maria Island (~1,000 individuals), Bruny Island (~500 individuals), and mainland Tasmania on Tinderbox Peninsula near Bruny Island (<100 individuals), as well as a small population in the northeast on Flinders Island (Bryant 2010). Although much of their habitat is protected, within the past 18 yr their population has declined by 60%, to ~1,500 birds (Bryant 2010). Remaining Forty-spotted Pardalote habitat is exclusively second-growth forest, which typically has limited nest-cavity availability (Newton 1994, Wiebe 2011). Strong competition for cavities often arises in cavity-limited systems (Heinsohn et al. 2003, Dhondt 2011), and competition with Striated Pardalotes (*Pardalotus substriatus*) is a potential threat to Forty-spotted Pardalotes (Woinarski and Rounsevell 1983).

Competition for nest cavities is common within communities of cavity-nesting birds (Martin and Eadie 1999, Dhondt 2011). The combination of limited cavity availability and strong selection pressure toward predator-safe cavities (e.g., those with small entrances, deep chambers, and high above the ground) results in direct competition for high-quality cavities (Nilsson 1984, Newton 1994). Although competition often excludes weaker species or individuals from high-quality resources, sustained competition for nest cavities is relatively common among closely matched cavity-nesting birds (Martin et al. 2004, Dhondt 2011). Weaker competitors for nest cavities may be forced to use poor-quality cavities (Kempanaers and Dhondt 1991), be prevented from acquiring a cavity (Dhondt and Adriaenson 1999), have their cavities usurped (Brazill-Boast et al. 2011), or may even be killed in conflict (Merilä and Wiggins 1995). These impacts can have population-level consequences, and competition for nest sites is a major threat to some endangered birds (Minot and Perrins 1986, Cade and Temple 1995, Cooper et al. 2007).

In competitive interactions, larger species usually dominate because body size is related to strength, weaponry, and cost of conflict (Persson 1985, Jennions and Backwell 1996). But in closely matched competitors, size differences may be overcome by aggressiveness, residency advantage, or shifts in the value of the resource to either competitor caused by parental investment or the difficulty of evicting eggs or nestlings (Slagsvold 1975, 1978, Gowaty 1981, Krist 2004). For example, Ingold (1998) found that an aggressive species, the European Starling (*Sturnus vulgaris*; 60–96 g), was able to evict a species twice its size, the Northern Flicker (*Colaptes auratus*; 110–160 g), from 27 of 40 nests at a site in Ohio, USA. For several cavity-nesting birds, the nest-building and egg-laying stages experience the highest takeover rates compared with later stages (Slagsvold 1975, Knight and Temple 1986). Possibly, the presence of nestlings complicates nest takeover because of the need for intruders to eject or build over the top of moving nestlings, which creates a strong discrepancy in the value of the resource between competitors (Krist 2004). Thus, the nesting stage may influence vulnerability to takeover for some species.

Striated Pardalotes (13.6 ± 0.7 g [SD]) compete with Forty-spotted Pardalotes (11.2 ± 1.2 g) for both nest sites and food (Rounsevell and Woinarski 1983, A. B. Edworthy personal observation). In contrast to Forty-spotted Pardalotes, Striated Pardalotes are common generalists, distributed throughout much of Australia (Woinarski and Bulman 1985, Birdlife International 2012). Woinarski and Bulman (1985) found that Forty-spotted Pardalotes were more frequently the aggressor in competitive interactions within their foraging territories, and concluded that Forty-spotted Pardalotes were dominant over Striated Pardalotes. However, I observed Striated Pardalotes (Striateds) evicting Forty-spotted Pardalotes (Forty-spotteds) from nest cavities. Because nest cavities are a discrete, limited resource, the outcome of contests for this resource can be easily assessed and offers the opportunity to assess dominance between pardalote species more clearly. The 2 species compete for similar cavities, though Striateds more frequently use cavities in living wood, which provide a more stable microclimate than those in dead wood, and Forty-spotteds are more likely to use cavities with entrances inclined above the vertical, which increases their exposure to rain (Woinarski and Bulman 1985, Wiebe

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FIGURE 1. Examples and consequences of competition for nest cavities between Forty-spotted and Striated pardalotes in southeastern Tasmania, Australia, 2013–2015. (**A**) Forty-spotted Pardalotes in aerial combat on Bruny Island, Tasmania, Australia (Photo credit: Alfred Schulte). (**B**) Striated Pardalote defending a recently usurped Forty-spotted Pardalote nest cavity (Photo credit: Mick Brown). (**C**) Forty-spotted Pardalote eggs punctured and removed from a cavity by Striated Pardalotes (Photo credit: Amanda Edworthy).

2001). Both species are socially monogamous, raise 1–2 broods per year, and primarily nest in tree cavities (or nest boxes), but occasionally use ground burrows (Higgins and Peter 2002). Conflict for nest cavities (Figure 1A) arises during the beginning of the breeding season in mid-August and can last through to early December when the last of the Striateds initiate breeding (A. B. Edworthy personal observation). Intruding Striateds inspect a cavity, perch at the entrance (or sit on top of the box), and sometimes call (Figure 1B). Forty-spotteds defend their nests by chasing off intruders repeatedly, with both members of the pair involved in nest and territory defense. Both conspecific and heterospecific conflict occur, and may result in energy loss, delayed breeding, nest takeover, and loss of eggs (Figure 1C). Forty-spotteds are resident in Tasmania and initiate breeding up to 3 weeks earlier than Striateds, which are at least partially migratory (Woinarski and Bulman 1985, Higgins and Peter 2002). As a result, competition from Striateds often occurs after Forty-spotteds have established nests, and the influence of breeding stage on competitive interactions may have important consequences for Forty-spotted Pardalote populations.

I use a 2-yr study of pardalote breeding biology to investigate the intensity and impact of interspecific competition for nest cavities on Forty-spotted Pardalotes. Study sites were selected in areas containing the 2 major island populations and largest remaining mainland Tasmanian population of Forty-spotted Pardalotes, and thus allow assessment of competition as a threat across much of their distribution. In this paper, I: (1) report the frequency and timing of Forty-spotted Pardalote nest takeovers by Striated Pardalotes, (2) use a model presentation experiment to investigate relative levels of nest-defense aggression by Forty-spotted and Striated pardalotes in response to heterospecific and conspecific competitors, and (3) test whether nest defense by pardalotes increases during the egg and nestling periods.

METHODS

Study Sites

I conducted fieldwork in dry coastal forests and woodlands of Maria Island (5 patches, 2–19 ha; 42.65°S, 148.05°E), Bruny Island (8 patches, 4–15 ha; 43.10°S, 147.36°E), and Tinderbox Peninsula (4 patches, 5–20 ha; 43.04°S, 147.32°E), Tasmania, Australia. Patches were sections of forest containing *Eucalyptus viminalis* trees, surrounded by either native forest or cleared farmland. Some patches were dominated by *E. viminalis*, while others contained a mix of *E. viminalis*, *E. pulchella*, *E. globulus*, *E. obliqua*, *E. ovata*, and *E. amygdalina* trees (Table 1, Figure 2). For this

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TABLE 1. Summary of site characteristics, number of pairs located at each site, and number of takeovers per nesting attempt (including only attempts that were monitored starting before eggs were laid) of Forty-spotted and Striated pardalotes in southeastern Tasmania, Australia, 2013–2015. Forest types included "viminalis," which was dominated by *Eucalyptus viminalis* (white gum trees), the main forage tree for Forty-spotted Pardalotes, and "mixed," which included a mix of *Eucalyptus* tree species including *E. viminalis*, *E. globulus*, *E. pulchella*, *E. obliqua*, *E. amygdalina*, and/or *E. ovata*. Striated Pardalotes were the usurpers in all Forty-spotted Pardalote nest takeover events, except for a single takeover at Maria Island Isthmus by Tree Martins (not shown).

		Forty-spotted Pardalote				Striated Pardalote			
Site grouping (area [ha])	Forest type	No. pairs 2013	No. pairs 2014	No. attempts (attempts in nest boxes)	No. takeovers (% of attempts)	No. pairs 2013	No. pairs 2014	No. attempts (attempts in nest boxes)	No. takeovers
Maria Island									
Isthmus (17)	Viminalis	19	16	43	0 (0%)	1	0	1	0
North (19)	Mixed	7	9	27	0 (0%)	5	7	7	0
Total		26	15	70	0 (0%)	6	7	8	0
Bruny Island									
Waterview Hill (25)	Viminalis	30	31	88 (78)	15 (17%)	21	24	61 (60)	0
Murrayfield (29)	Mixed	6	16	19 (2)	1 (5%)	5	9	8 (4)	0
Total		36	47	107 (80)	16 (15%)	26	33	69 (64)	0
Tinderbox Peninsula (mainland Tasmania)									
Howden (17)	Viminalis	1	2	2	0 (0%)	5	5	6	0
Tinderbox Ridge (40)	Mixed	13	9	16 (2)	3 (18%)	12	7	8 (1)	0
Total		14	11	18 (2)	3 (17%)	17	12	14 (1)	0
Grand total		76	73	195 (82)	19 (10%)	49	52	91 (65)	0

study, patches were grouped into sites, which reflected their geographical proximity and forest type (Table 1). There were 2 sites on Maria Island: Isthmus, a single patch of *E. viminalis*–dominated forest; and North Maria Island, composed of 4 patches of mixed forest in the north of the island. There were 2 sites on Bruny Island: Waterview Hill, composed of 2 patches of *E. viminalis*–dominated forest on opposite sides of Waterview Hill; and Murrayfield, composed of 5 patches of mixed forest on Murrayfield Farm. Finally, there were 2 sites on mainland Tasmania: Howden, a single patch of *E. viminalis* within the Peter Murrell Nature Reserve, at the base of Tinderbox Peninsula; and Tinderbox Ridge, a string of small clumps or individual *E. viminalis* trees spread across the length of the ridge. Bruny Island and Tinderbox Peninsula are separated by a 1.4-km channel, and Forty-spotted Pardalotes may disperse from the larger population on Bruny Island to Tinderbox Peninsula, which supports 1 of the 2 remaining mainland Tasmanian populations. Maria Island is 65 km NE of Bruny Island, and separated from mainland Tasmania by a 4-km channel. Sixty percent of Forty-spotted Pardalote habitat is protected in reserves, including Maria Island National Park, which protects the whole of Maria Island; 2 state reserves on Tinderbox Peninsula, including the Howden study site (Peter Murrell Nature Reserve) and Magazine Reserve on Tinderbox Ridge; and Pierson's Point, a municipal reserve at the tip of Tinderbox Peninsula (Kingborough Council; Bryant 2010). On Bruny Island, the Murrayfield sites are the property of the

FIGURE 2. Habitat in southeastern Tasmania, Australia, at (**A**) the Isthmus site on Maria Island, dominated by *Eucalyptus viminalis* (Photo credit: Amanda Edworthy), and (**B**) a Murrayfield patch on Bruny Island, composed of mixed *Eucalyptus* species (Photo credit: Linda Edworthy).

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Indigenous Land Corporation, and the Waterview sites are privately owned.

Both pardalote species were common in the study sites. Although these species occasionally nest in ground burrows, only 3 Striated Pardalote pairs nested in burrows, with all other nests in natural tree cavities or nest boxes (Table 1). Most nests in boxes were in the Waterview Hill study site, where 100 nest boxes were installed in 2008 (Table 1). However, there were also 2 existing nest boxes on Tinderbox Peninsula, 1 of which was used. In July 2013, I installed an additional 153 boxes (46 on Maria Island, 51 on Bruny Island, and 56 on mainland Tasmania), but the time lag for box uptake by pardalotes is >2 yr. Only 8 of these new boxes were used by pardalotes, all within a single patch in the Murrayfield site.

Nest Monitoring for Breeding and Takeover Rates

I located nests of Forty-spotted and Striated pardalotes in both nest boxes and natural cavities by searching potential nest sites and by following birds to their cavities during August to January in 2013–2015. To provide an estimate of pardalote breeding density at each site, I report all pairs located, regardless of whether they were found early enough in the nesting cycle (prelaying) to use in the takeover analysis (Table 1). However, the number of Striated Pardalotes was likely underestimated in the Murrayfield, Howden, and Tinderbox Ridge sites due to large site areas and lower search effort for Striated Pardalote nests.

To assess nesting stage, identity of adult birds defending the nest, and interactions between Forty-spotted and Striated pardalotes at nest sites, nests were monitored every 4 days using ladders for cavities and nest boxes up to 7 m high, climbing ropes for cavities up to 30 m high, or behavioral observations from the ground for inaccessible cavities. Where possible, nest contents were inspected using a video camera on a flexible stalk (Burrowcam; Faunatech, Mount Taylor, Victoria, Australia). Nest takeovers were defined as cases in which: (1) a nest site was occupied by a pardalote pair (building, defending, laying, incubating, or feeding nestlings); (2) aggressive interaction (e.g., chasing) was observed between the resident pair and an intruder of a different species; and (3) on subsequent checks, the intruder species had ownership of the nest site (e.g., building, defending, or laying). Forty-spotted Pardalotes were color-banded to identify individuals; 124 of 156 pairs (79%) had at least 1 banded member during the study. Because Forty-spotted Pardalotes are socially monogamous during the breeding season, I could generally distinguish between pairs. Fourteen of the 20 pairs who had their cavities usurped had at least 1 banded member, and I continued to monitor their activity following takeover to determine whether they renested elsewhere.

Model Presentation Experiment

I conducted a model presentation experiment to assess relative levels of aggression toward heterospecific and conspecific intruders by Forty-spotted Pardalotes ($n = 15$ nests; 12 boxes and 3 natural cavities) and Striated Pardalotes ($n = 16$ nests; 15 boxes and 1 natural cavity). At each nest I conducted 3 trials, presenting freeze-dried specimens ("dummies" or "models") of a Forty-spotted Pardalote, a Striated Pardalote, and a noncompetitor control. The models were perched in a life-like position with wings folded. Intruding competitors typically land at the cavity entrance, display (Striated only), and often call. To approximate this behavior, at nest boxes I used a telescoping pole to place the model (perched on a small wire stand) on top of the box, and at natural cavities I perched the model on a wire hanger and placed it within 1 m of the cavity entrance. To reduce the response of target pairs to my presence, I placed the model while both members of the pair were foraging away from the nest tree. For conspecific and heterospecific models I used 2 specimens of each pardalote species, and for noncompetitor models I used 1 of either Grey Fantail (*Rhipidura albiscapa*) or Silvereye (*Zosterops lateralis*), which are open-cup nesters and forage in the understory. To randomize trial order, I used the "sample" function in the statistical program R, generating a random list of numbers from 1 to 6 for the 6 possible trial orders, with each trial order represented 2 or 3 times for both Forty-spotted and Striated pardalote nests (blocked randomization; R Development Core Team 2012). Subsequent trials were conducted within 1–3 days of each other.

I started the trial when at least 1 member of the resident pair returned to the nest tree. Trials ended after 10 min, or when the pardalotes pecked the model repeatedly or knocked it to the ground. During each trial, I estimated the distance of the resident birds to the model and recorded their behavior, including: (1) no response; (2) agitation: short hops and rapid wing extensions; (3) aggressive approach: swoop toward or hover at the model; (4) display: wings and tail fanned, crest raised; and (5) contact: direct attack with feet or bill. I could not consistently distinguish between sexes or individuals because their bands were too small to see during the experiment and both species lack obvious sexual dimorphism, so I used the strongest response (closest approach and most aggressive behavior) from each pair for the analysis. The trials were conducted within an 8-week period (September 28–November 18, 2013), using pairs that were nesting simultaneously in different locations, so I was confident that each of the pairs used in the experiment was unique; where possible, this was confirmed by identification of color-banded birds.

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Statistical Analysis

I used a linear mixed-effects model to estimate relative aggression by Forty-spotted and Striated pardalotes toward competitor dummies and across nest stages. All variables of interest and their potential interactions were included in a single model. Minimum distance of approach to the competitor dummy was used as the measure of aggression (response variable), and was transformed by ($\ln(x + 1$ cm$)$) to normalize the distribution. Fixed effects included species of nest defender (Forty-spotted Pardalote or Striated Pardalote), competitor dummy type (heterospecific, conspecific, or noncompetitor [Grey Fantail or Silvereye]), and nest stage (prelaying, or eggs or nestlings present), as well as the 2-way interactions of species of nest defender with competitor dummy type and nest stage, and the 3-way interaction of species of nest defender, competitor dummy type, and nest stage. The "prelaying" category included the period from the beginning of nest building to the start of laying. Nest ID was included in the model as a random effect to account for repeated sampling of individual pairs (3 competitor dummies presented once each per pair; Laird and Ware 1982). After log-transforming the dependent variable, both the assumptions of homogeneity of variance (Levene's test: $F = 1.29$, $P = 0.24$) and normality (Shapiro-Wilk test: $W = 0.98$, $P = 0.30$) were met and verified by examining residual vs. fitted values and Q-Q plots. Model fit was assessed using marginal R^2 to describe the proportion of variance explained by the fixed factors alone, and conditional R^2 to estimate the proportion of variance described by the fixed and random effects together (Nakagawa and Schielzeth 2013).

In addition to using the closest distance of approach to the competitor dummy as a measure of aggression, I calculated the frequency of the maximum level of aggression displayed in each trial type, ordered from least to most aggressive as (1) no response, (2) aggressive approach, including swoop or hover, and (3) display or contact. Display and contact were grouped together because displays were used only by Striated Pardalotes, and were a highly aggressive response (usually within 5–15 cm of the model). I used chi-square tests to assess differences in the frequencies of responses to competitor dummies between the 2 pardalote species. Values are reported as mean ± standard error (SE). All analyses were done using R, including the nlme package (R Development Core Team 2012, Pinheiro et al. 2013).

RESULTS

Frequency and Timing of Nest Takeovers

Striated Pardalotes usurped the nests of Forty-spotted Pardalotes in 19 of 192 ($\sim$10%) nesting attempts (Table 1). There were no cases of Forty-spotted Pardalotes taking over Striated Pardalote nests ($n = 91$ nests). Takeover rates were highest on mainland Tasmania ($\sim$17%, $n = 18$ nests) and Bruny Island ($\sim$15%, $n = 104$ nests). On Maria Island, there were no takeovers by Striated Pardalotes, but Tree Martins (*Petrochelidon nigricans*) took over a single Forty-spotted Pardalote nest ($n = 70$ nests; Table 1). Eighty percent of takeovers by Striated Pardalotes (and the single takeover by a Tree Martin) took place while Forty-spotted Pardalotes were nest building, prior to egg laying (16 of 20 takeovers); in the remaining 20% (4 cases), Striated Pardalotes punctured and removed Forty-spotted Pardalote eggs (Figure 1C), or crushed eggs in the nest and then removed shell fragments and replaced some of the nest material. Four of the 14 banded Forty-spotted Pardalote pairs (29%) that experienced takeovers by Striated Pardalotes or Tree Martins nevertheless managed to breed successfully in an earlier or later attempt within the same breeding season. Five pairs had their nests usurped during their second nesting attempt. Four of 14 pairs (29%) with banded individuals renested in new locations: 2 pairs moved from nest boxes into natural cavities nearby, 1 pair moved between natural cavities, and the last pair moved from one nest box to a second box on the same tree (2 of these attempts were successful).

During all takeovers, I observed Forty-spotted Pardalotes chasing intruding Striated Pardalotes prior to takeover. During 1 takeover, Striated and Forty-spotted pardalotes were observed engaging in frequent chases and displays (e.g., 20 chases hr^{-1}) over a period of 2 days.

Model Presentation Experiment

The closest distance of approach to the competitor dummy was influenced by both species of nest defender and competitor type, but there was no effect of nest stage (Table 2, Figures 3 and 4). The fixed effects explained 22% of the variance (marginal $R^2 = 0.221$), and, by taking pair ID into account as a random effect, the full model explained 43% of the variation (conditional $R^2 = 0.433$).

Striated Pardalotes approached to within similar distances of heterospecific and conspecific competitor dummies (0.05 ± 0.03 m and 0.04 ± 0.03 m, respectively; $F_{1,15} = 0.02$, $P = 0.88$; Figure 3). Forty-spotted Pardalotes approached conspecific models more closely than heterospecific dummies (0.01 ± 0.00 m vs. 0.06 ± 0.04 m; $F_{1,14} = 6.86$, $P = 0.02$), which suggests that Striated Pardalotes were seen as the more threatening opponent by Forty-spotted Pardalotes (Figure 3). Noncompetitor controls were not approached as closely as heterospecific ($F_{1,26} = 5.48$, $P = 0.03$) or conspecific dummies ($F_{1,25} = 28.30$, $P < 0.001$) by either species of defending pardalote (Figure 3). The effect of nest stage was nonsignificant across species and competitor dummy type, indicating no change in nest defense aggression toward any competitor after eggs were

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TABLE 2. Analysis of variance (ANOVA) results for a generalized linear mixed-effects model predicting distance approached to the competitor dummy (transformed by ln($x + 1$)) as a function of species of nest defender (Forty-spotted Pardalote, $n = 15$; or Striated Pardalote, $n = 16$), competitor dummy type (conspecific, heterospecific, and noncompetitor control [Grey Fantail or Silvereye]), nest stage (prelaying [$n = 33$], or eggs or nestlings present [$n = 29$]), and all relevant interactions for Forty-spotted and Striated pardalotes in southeastern Tasmania, Australia, 2013. Nest ID was included in the model as a random factor to account for repeated trials at individual nests. Bold font denotes statistical significance ($P < 0.05$).

Model term	df	*F*	*P*
Intercept	1 and 52	170.67	**<0.001**
Species	1 and 29	0.04	0.84
Competitor type	2 and 52	11.09	**<0.001**
Nest stage	1 and 52	1.60	0.21
Species*Competitor type	2 and 52	3.66	**0.03**
Species*Nest stage	1 and 52	0.01	0.93
Competitor type*Nest stage	2 and 52	1.19	0.31
Species*Competitor type *Nest stage	2 and 52	0.16	0.85

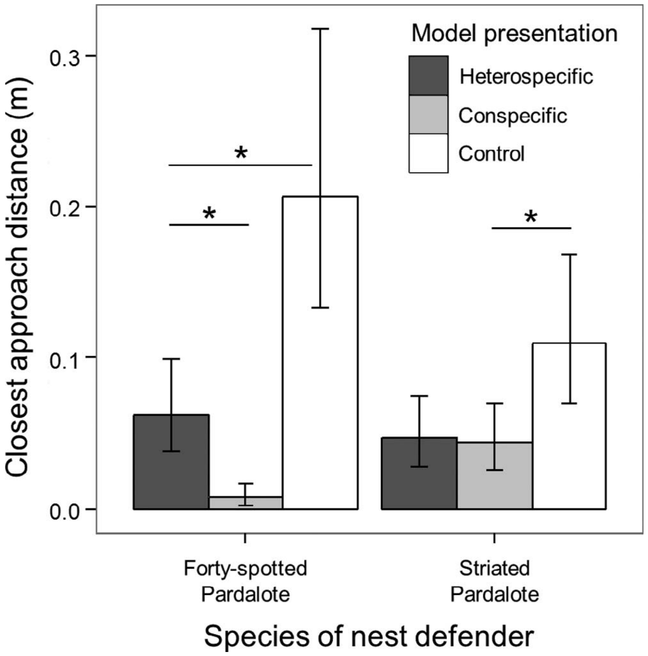

FIGURE 3. Mean closest approach distance (m) of Forty-spotted Pardalotes (light gray bars; $n = 15$ trials per model) and Striated Pardalotes (dark gray bars; $n = 16$ trials per model) to competitor dummies (heterospecific, conspecific, and noncompetitor control [Grey Fantail or Silvereye]) placed at nest sites in southeastern Tasmania, Australia, 2013. Means were averaged across nest stages (prelaying, eggs present, and nestlings present). The means and standard errors (error bars) were back-transformed from log-transformed values of approach distance (ln(x + 1 cm)). Smaller values of approach distance (lower on the *y*-axis) were interpreted as higher levels of aggression. Asterisks denote significant differences ($P < 0.05$) between responses to competitor dummy types within each species of nest defender.

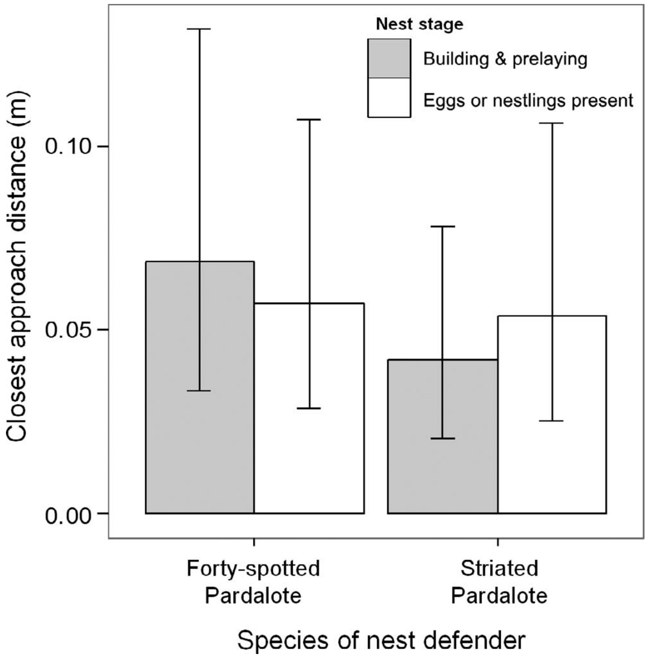

FIGURE 4. Effects of nesting stage (prelaying [$n = 33$], or eggs or nestlings present [$n = 29$]) on mean closest distance of approach (m) by Forty-spotted and Striated pardalotes to competitor dummies (set to heterospecific in this graph) placed at nest sites in southeastern Tasmania, Australia, 2013. The means and standard errors (error bars) were back-transformed from log-transformed values of approach distance (ln(x + 1 cm)). Smaller values of approach distance (lower on the *y*-axis) were interpreted as higher levels of aggression. The effect of nest stage on approach distance was nonsignificant ($F = 1.60$, $P = 0.21$), as was the interaction between species and nest stage ($F = 0.01$, $P = 0.93$) and the 3-way interaction of species, nest stage, and competitor type ($F = 0.16$, $P = 0.85$).

laid for either Forty-spotted or Striated pardalotes (Table 2, Figure 4).

Both Forty-spotted and Striated pardalotes made contact with intruding competitor dummies by pecking or grabbing with their claws, but only Striated Pardalotes used displays (wings and tail fanned, crest raised), typically within 5–15 cm of the model. Patterns in the most aggressive behavior displayed mirrored patterns of aggression seen in closest approach distance: Striated Pardalotes displayed or made contact with both conspecifics and heterospecifics in the same percentage of trials (75%; $n = 16$ trials, $\chi^2 = 0.00$, $P = 1.00$), whereas Forty-spotted Pardalotes made contact more frequently with conspecifics (87%) than with heterospecifics (40%; $n = 15$ trials, $\chi^2 = 3.90$, $P = 0.048$; Figure 5). Both Forty-spotted and Striated pardalotes were less aggressive toward noncompetitor dummies in their use of displays and/or contact (20% vs. 63%, respectively, in Forty-spotted Pardalotes [$n = 15$ trials, $\chi^2 = 7.52$, $P = 0.006$], and 19% vs. 75% in Striated Pardalotes [$n = 16$ trials, $\chi^2 = 13.71$, $P < 0.001$]; Figure 5).

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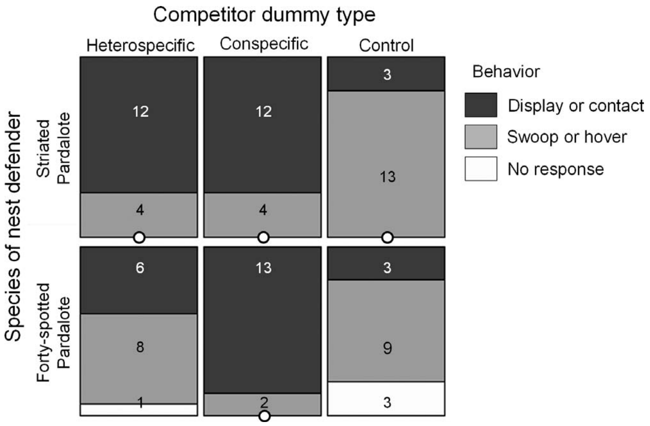

FIGURE 5. Relative frequencies of the most aggressive behavior displayed by Forty-spotted Pardalotes ($n = 15$ trials per competitor dummy type) and Striated Pardalotes ($n = 16$ trials per competitor) in response to presentations of 3 competitor dummies (heterospecific, conspecific, and noncompetitor control [Grey Fantail or Silvereye]) placed at nest sites in southeastern Tasmania, Australia, 2013. Circles represent frequencies of zero.

DISCUSSION

The results of this study show that competition for nest cavities reduces breeding opportunities for Forty-spotted Pardalotes. Competition for cavities is an important factor to consider in conservation management of the species. Striated Pardalotes (Striateds) were the dominant competitor for nest cavities, displaying greater aggression toward heterospecifics than Forty-spotted Pardalotes (Forty-spotteds), and evicting ~10% of Forty-spotted breeding pairs across all study sites. However, there was strong variation in takeover rates among regions, with no usurpations on Maria Island and high rates on Bruny Island and mainland Tasmania. Takeovers had a substantial impact on Forty-spotted breeding success. Sixteen of 20 pairs that had their nests usurped produced no offspring for the year; just 4 pairs nested successfully in an earlier or subsequent attempt in a new location. While these results show a clear negative impact on Forty-spotted Pardalotes, the impact of Forty-spotteds on Striated Pardalotes is uncertain. If Striated usurpers save nest-building time and energy by taking over Forty-spotted nests (both species add and reuse nest material in cavities), then their interaction might be kleptoparasitism rather than competition (Kappes 1997). However, probable costs to Striateds include energy spent usurping Forty-spotted nests (e.g., frequent chases over up to 2 days), and likely reduced or delayed access to cavities that are occupied early in the breeding season by Forty-spotteds. These impacts are forms of interference and exploitative competition, respectively.

All remaining Forty-spotted Pardalote habitat is second-growth forest, and limited cavity availability in these forests may intensify competition for nest sites (e.g., Brazill-Boast et al. 2013). However, relative population densities of the 2 pardalote species also appeared to have a strong impact on takeover rates. Takeovers were most frequent in the Bruny Island (where nests were in boxes and natural cavities) and mainland Tasmania regions (all nests in natural cavities, except 1), where Striateds usurped ~15–17% of nests. These areas had greater abundances of Striated Pardalotes than Maria Island, where all nests were in natural cavities and there were no takeovers by Striateds. At the site level, Waterview, on Bruny Island, had the highest frequency of takeovers (15 of 88 nesting attempts) and also had the highest densities of both Forty-spotted (1.20–1.24 pairs ha^{-1}) and Striated pardalotes (0.84–0.96 pairs ha^{-1}). Waterview was also the only site in which most nests were in boxes, and increased densities of both species in response to nest boxes may have resulted in increased competition. Further research is needed to examine the interacting effects of relative population densities, nest-site availability, and habitat quality on competition. Nest box experiments that monitor breeding density, nest success, and interspecific takeovers before and after occupation of nest boxes, and across sites that vary in forest type and cavity availability, are needed to examine the effects of nest boxes on population density and competition.

Striated Pardalotes displayed equally aggressive responses toward both heterospecific and conspecific dummies, suggesting that the perceived relative threat or risk of conflict was similar between both competitor types. Conversely, aggressive responses by Forty-spotted Pardalotes were weaker toward heterospecific dummies (40% of trials involved contact, $n = 15$) than toward conspecific dummies (87% involved contact, $n = 16$). I interpret the weaker response of Forty-spotted Pardalotes toward Striated Pardalotes as caution in the face of a relatively threatening competitor. Alternatively, Striated Pardalotes may present less risk to Forty-spotted Pardalotes (i.e. Striated Pardalotes may not be a significant competitor for nest sites, or may be easily deterred) and thus may require less response. However, my observations of takeovers and extensive interspecific chasing and displays centered on nest cavities confirm that there is real contest between the two pardalote species for nest sites. A similar study of interspecific aggression between endangered Gouldian Finches (*Chloebia gouldiae*) and Long-tailed Finches (*Poephila acuticauda*) showed that the subordinate Gouldian Finch was more reluctant to approach Long-tailed Finch dummies than Gouldian Finch dummies (Pearce et al. 2011). In this case, interspecific competition resulted in reduced fledging rates and breeding density of Gouldian Finches (Brazill-Boast et al. 2011, 2013).

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Although differences in competitive strength can result in the exclusion of weaker competitors from high-quality habitat (Kempenaers and Dhondt 1991, Robinson and Terborgh 1995, Martin and Eadie 1999), sustained competition for cavity resources appears to be relatively common among cavity-nesters with similar body sizes (e.g., Slagsvold 1975, Meek and Robertson 1994). Competitors for nest cavities employ strategies to reduce the degree of competition or to change the balance of competitive strength through subtle shifts in cavity selection (e.g., Robles and Martin 2013) or early timing of breeding (Wiebe 2003). To some extent, Forty-spotted Pardalotes appear to use lower-quality cavities than Striated Pardalotes—for example, those in dead rather than living wood—although the effects of cavity characteristics on breeding success have not been tested (Woinarski and Bulman 1985). As residents, Forty-spotteds are also able to start breeding earlier than Striateds, and they may defend their nests more aggressively with greater investment into eggs and nestlings, or may gain a residency advantage independent of nest defense aggression.

Seventy-nine percent of takeovers of Forty-spotted Pardalote cavities by Striated Pardalotes ($n = 19$) occurred before the Forty-spotted Pardalotes started laying (during the nest-building period or between nest-building and laying). While some species are capable of usurping the nests of their competitors at any stage of the nesting period by removing or building over the top of eggs or nestlings (e.g., House Wrens [*Troglodytes aedon*]; Doherty and Grubb 2002), for many species the majority of takeovers appear to occur before eggs are laid or during the laying period (Slagsvold 1975). Forty-spotted Pardalotes start nesting earlier on average than Striated Pardalotes, so differences in takeover risk among nest stages may affect cavity acquisition at the population level in these species. Increasing aggression across nest stages (e.g., due to increased parental investment) is one possible explanation for the decreased takeover rates following egg laying (Trivers 1972). However, there was no change in nest-defense aggression by either pardalote species after egg laying. Thus, the declining risk of takeover was likely due to other factors related to residency advantage. For example, the presence of eggs or nestlings may increase the difficulty of takeover because of the need to eject nest contents or build over the top of nestlings (Krist 2004). Regardless of the mechanisms involved, early onset of breeding seems to force Forty-spotted Pardalotes into frequent conflict with Striated Pardalotes searching for nest sites. It is uncertain whether Forty-spotteds benefit from early cavity acquisition by successfully defending at least some nest sites that would otherwise be claimed by Striated Pardalotes, or whether they suffer high costs of nest building and egg laying in cavities that will inevitably be usurped.

Management of competitors for nest sites can be a key conservation strategy for endangered cavity- and burrow-nesting species (Cade and Temple 1995). Butchart et al. (2006) found that, of 7 obligate cavity-nesters on the brink of extinction during 1994–2004, 4 were likely saved because of the control or removal of competitors for nest sites, or the provision of nest boxes to reduce competition. While removal of Striated Pardalotes is not an option because they are native species, restoration of nest sites through habitat protection and nest box addition is a promising conservation strategy for Forty-spotted Pardalotes. Over multiple decades or centuries, regeneration of mature, complex forests will help to restore the availability of cavities with a range of characteristics to allow partitioning of cavities among competitors (Lindenmayer and Franklin 1997, Robles and Martin 2013). Over shorter time periods, provision of nest boxes may alleviate interspecific competition or create alternative nesting sites for displaced pairs.

However, my results suggest that increased densities at sites with nest boxes may also result in increased interspecific competition. In some cases, increased competition outweighs the benefits of nest boxes, and can have negative effects on the breeding success of the target species (e.g., Finch 1990). In the United States, the decline of Bewick's Wrens (*Thryomanes bewickii*) was linked to increasing densities of House Wrens, which destroy multiple nests of competitors in their territories, including those with eggs or nestlings (Kennedy and White 1996). Where nest boxes result in increased densities of aggressive competitors such as House Wrens, the net breeding success of their competitors may suffer (Finch 1990). But, unlike House Wrens, Striated Pardalotes do not destroy multiple nests of other species in their territories and are not considered an unusually aggressive species. Rather, the asymmetric tendency for Striateds to be the usurpers is likely due in part to the earlier commencement of breeding and occupation of nest sites by Forty-spotteds. Nonetheless, it will be important to assess the net effects of nest box addition on Forty-spotted Pardalotes, considering the benefits of increased breeding density and nest success relative to the costs of increased competition.

Nest-box addition has had a clearly positive effect for many threatened cavity-nesting birds, and, in systems in which cavity limitation motivates interspecific competition, we would expect nest-box addition to reduce competition for cavities (e.g., Brazill-Boast et al. 2013). However, given the possibility of increased competition with increasing population densities, nest-box design and placement should minimize competition by taking the ecology and behavior of individual species into account (Finch 1990). Distribution of boxes across mixed species and *Eucalyptus viminalis*–dominated forests might allow for greater habitat partitioning among pardalote species (Woinarski and Rounsevell 1983). Fine-scale cavity-selection preferences such as height or entrance diameter can

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also be used to reduce competition for nest boxes (Robertson and Rendell 1990, Aitken and Martin 2008). A 6-mm difference in nest-box entrance diameter excludes Eurasian Great Tits (*Parus major*) and allows access by their subordinate competitors, Blue Tits (*Cyanistes caeruleus*; Dhondt and Adriaensen 1999). Nest boxes currently in use for pardalotes allow access by both species (entrance diameter = 28–30 mm), but smaller entrance diameters may exclude Striated Pardalotes. Further experiments are needed to assess the impacts of nest-box design, entrance diameter, and forest context on densities and competition between pardalote species.

In general, competition is an important factor to consider in evaluating the effects of habitat management strategies on pardalotes. But the impact of competition must also be considered in the broader context of demographic rates and other threats to Forty-spotted Pardalotes to determine its relevance to their population trajectory.

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