



Original Article

# Predator defense is shaped by risk, brood value and social group benefits in a cooperative breeder

Niki Teunissen<sup>a,\*</sup>, Sjouke A Kingma<sup>b,\*</sup> and Anne Peters<sup>a,c</sup>

<sup>a</sup>School of Biological Sciences, Monash University, 25 Rainforest Walk, Clayton, Victoria 3800, Australia, <sup>b</sup>Behavioural Ecology Group, Department of Animal Sciences, Wageningen University and Research, De Elst 1, 6708 WD Wageningen, The Netherlands, and <sup>c</sup>Max Planck Institute for Ornithology, Vogelwarte Radolfzell, Schlossallee 2, D-78315 Radolfzell, Germany

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Predation is a major cause of mortality and nest failure in birds. Cooperative predator defense can enhance nest success and adult survival but, because it is inherently risky, dynamic risk assessment theory predicts that individuals modify defense behavior according to the risk posed by the predator. Parental investment theory, on the other hand, predicts that reproductive payoffs (brood value) determine investment in nest defense. We propose that, in cooperative breeders, fitness benefits deriving from the survival of other group members may additionally influence defense behavior (social group benefits theory). We tested predictions of these theories in the cooperatively breeding purple-crowned fairy-wren, *Malurus coronatus*, where brood value is higher for breeders, but social group benefits more important for helpers. We recorded experimentally induced individual defense behaviors in response to predator models presented near nests, representing differing levels of threat to nests and adults. As predicted, 1) individuals engaged in less risky defenses when encountering a more dangerous predator (dynamic risk assessment theory); 2) individuals defended older broods more often, and breeders defended more than helpers (parental investment theory); and 3) helpers were more likely to respond to a predator of adults (social group benefits theory). Our findings highlight that predator defense in cooperative breeders is complex, shaped by the combination of immediate risk and multiple benefits.

**Keywords:** altruism, antipredator behavior, cooperation, helping, nest defense, predation.

## INTRODUCTION

Predation is a major cause of adult mortality and reproductive failure in birds (Ricklefs 1969; Lima and Dill 1990; Menezes and Angelo Marini 2017). Individuals may engage in active predator defense by attacking, mobbing, or distracting predators and uttering frequent calls (Montgomerie and Weatherhead 1988; Arnold 2000; Caro 2005; Graw and Manser 2007; Groenewoud et al. 2019). Parental investment theory predicts that the intensity of such nest defense increases with increasing fitness benefits associated with the survival of the current brood (Trivers 1972; Montgomerie and Weatherhead 1988). Indeed, nest defense intensity has been found to increase with increasing brood value (e.g., larger, older, or higher-quality brood; Olendorf and Robinson 2000; Rytönen 2002; Svagelj et al. 2012; van Asten et al. 2016).

However, predator defense is costly as it involves an increased risk of mortality and injury, lost foraging and mating opportunities, and

energy expenditure (Montgomerie and Weatherhead 1988; Dugatkin and Godin 1992; Feeney and Langmore 2015). Dynamic risk assessment theory, therefore, predicts that the intensity of nest defense will be lower when there are higher costs associated with defense, for example, when the risk of mortality associated with the predator is higher, or expected future reproduction is higher, and the potential fitness lost is, thus, greater (Montgomerie and Weatherhead 1988; Dugatkin and Godin 1992). In support of the latter, nest defense intensity has been found to increase with age and throughout the breeding season as future breeding opportunities decline (Barash 1980; Regelman and Curio 1983; Thornhill 1989). However, various studies have reported an apparent increase in defense intensity for predators posing a greater risk (Edelaar and Wright 2006; Graw and Manser 2007; Griesser 2009; Colombelli-Negrel et al. 2010a, 2010b; Dutour et al. 2016). But because these studies focused primarily on the vocal response by prey species, this does not necessarily reflect high risk-taking behavior. Instead, individuals may vary their defense strategy rather than intensity according to the type of predator, for example, increasing their vocal response but

Address correspondence to N. Teunissen. E-mail: niki.teunissen@monash.edu

keeping a greater distance from predators associated with greater risk (Swaigood et al. 1999; Strnad et al. 2012; Koberoff et al. 2013). This illustrates that when testing theories of predator defense, various types of defense need to be taken into consideration.

Cooperatively breeding species, in which subordinate individuals help a dominant breeding pair to raise their offspring instead of reproducing independently (Brown 1987; Cockburn 1998), provide a particularly interesting system to study the complexities of predator defense and to examine predictions from parental investment and dynamic risk assessment theories simultaneously. Helpers can improve nest defense against predators, as well as brood parasites, via increased vigilance or enhanced active defense through, for example, increased mobbing behavior (McGowan and Woolfenden 1989; Hailman et al. 1994; Boland 1998; Canestrari et al. 2009; Riehl 2011; Feeney et al. 2013). However, breeders and helpers generally have different stakes in the breeding attempt. First, breeders are expected to invest more in current relative to future reproduction. Additionally, they generally gain substantially greater genetic fitness benefits by raising their own offspring compared with helpers, especially in systems where groups can include nonkin (Riehl 2013), and helpers do not participate in reproduction. Therefore, breeders and helpers are predicted to engage differently in nest defense not only because of variation in risk posed by different predators but also as a result of variation in benefits associated with predator defense. Moreover, and importantly, individuals in cooperative groups may not only defend the brood but also protect group members when a predator poses a threat to adults (e.g. Francis et al. 1989; Garay 2009; Shen et al. 2017). Although this could potentially also be relevant in noncooperative socially monogamous species (individuals protecting their partner), increased protection of conspecifics has been proposed as a key driver of group formation (Du Plessis et al. 1995; Caro 2005; Jungwirth et al. 2015; Groenewoud et al. 2016). Protection of group members may, therefore, be an especially important reason for defense against predators in cooperative breeders (social group benefits theory).

Social group benefits vary within cooperative groups and may be more important for explaining predator defense behavior by helpers, for whom benefits associated with the social group may be greater than benefits directly associated with the brood. Depending on the social environment, individual helpers can obtain many different social benefits from group members, for example, through parental nepotism, breeding position inheritance, obtaining a mate, kin-selected benefits, or group augmentation (Ekman et al. 2000; Kokko et al. 2001; Kingma 2017). Although patterns of vigilance have been shown to vary at least to some extent with social benefits (presence of juveniles or kin) in several species (Griesser and Nystrand 2009; Santema and Clutton-Brock 2013; Bednekoff 2015; but see Wright et al. 2001), social benefits have surprisingly rarely explicitly been considered when attempting to understand how variation in more risky, active, predator defense is shaped in cooperatively breeding species (but see Griesser and Ekman 2005). In general, investigating helper contribution to active predator defense in cooperatively breeding species (as in, e.g., Maklakov 2002; Arnold et al. 2005; Griesser and Ekman 2005; Buintjes and Taborsky 2011; van Asten et al. 2016) may shed light on the adaptive benefits of group living and social structures in cooperative breeders.

Here, we test if combined predictions of the parental investment, dynamic risk assessment, and social group benefits theories (see Table 1 for an overview) can explain investment in predator defense in a cooperative breeder. To do so, we assess individual helper and breeder contribution to predator defense in response to

three predator models, representing 1) a predator of nests only, 2) a predator of nests and adults, 3) a brood parasite (a large threat to the nest but no threat to adults), and 4) a nonthreatening control. In our study species, the cooperatively breeding purple-crowned fairy-wren, *Malurus coronatus*, groups consist of a dominant breeding pair that is often accompanied by one or more nonbreeding male or female subordinates (range = 0–5 subordinates, mean number of male and female subordinates per group  $\pm$  standard error [SE] =  $0.5 \pm 0.1$  and  $0.4 \pm 0.1$ , respectively, for the current study; Kingma et al. 2010, 2011). Breeders and helpers differ in the benefits associated with raising the brood. Breeders are monogamous (extrapair paternity is rare: 4.4% of offspring; Kingma et al. 2009), whereas male and female helpers rarely gain parentage (1.8% and 0% of offspring respectively; Kingma et al. 2009) and vary in relatedness to the brood due to breeder turnover (i.e., breeder replacement as a result of mortality or divorce; Kingma et al. 2010, 2011). Consequently, both male and female breeders are on average more related to the brood than helpers ( $r = 0.5$  for 98% of breeders compared with 62% of helpers; Kingma et al. 2011). Conversely, social group benefits are expected to be comparatively more important for helpers than benefits associated with the brood. Although these also include kin-selected benefits, related breeders may additionally offer benefits through parental nepotism. Group members may further offer benefits to helpers through group augmentation or future reproduction (as unrelated opposite-sex group members represent potential future mates obtained through breeding position inheritance or by pairing with another subordinate to form a new territory; Hidalgo Aranzamendi et al. 2016; Teunissen et al. 2018). These social group benefits are, on average, greater for male helpers because they have greater chances of breeding position inheritance and are more philopatric, thus, staying on their natal territory for longer to reap those benefits (Kingma et al. 2010, 2011; Margraf and Cockburn 2013; Teunissen et al. 2018). If individuals in this species indeed simultaneously balance risk of injury/mortality, fitness payoffs of the current brood surviving, and fitness payoffs of adult group members surviving, we predict that 1) individuals engage in less risk-taking when a predator poses greater risk of injury; 2) individuals respond more strongly with increasing brood value (i.e., brood age and size); 3) breeders defend more intensely overall; 4) male helpers defend more intensely than female helpers; and 5) helpers defend relatively more strongly to predators of adults (Table 1).

## MATERIALS AND METHODS

### Study site and species

We studied a fully color-banded population of purple-crowned fairy-wrens that has been studied since 2005 at Australian Wildlife Conservancy's Mornington Wildlife Sanctuary in northwest Australia (S17°31' E126°6'). Purple-crowned fairy-wrens are riparian habitat specialists with stable year-round territories aligned linearly along watercourses (Rowley and Russell 1993). Only the dominant pair duets, providing a reliable cue to assign breeder status (Hall and Peters 2008), which our previous studies confirmed by parentage analyses (Kingma et al. 2009). Subordinates form stable queues for breeding position inheritance on the territory (Kingma et al. 2011), and subordinates of both sexes can assist the breeding pair to provision offspring. While they vary in offspring feeding rates (Kingma et al. 2010, 2011), here we use the term "helper" to refer to any subordinate.

**Table 1**

**Predictions for individual predator defense intensity based on the two main current theories for nest defense, and our proposed social group benefits theory for cooperative breeders. Predictions specific for purple-crowned fairy-wrens are given and whether these were supported in this study**

Theory	Nest defense predicted to increase when:	Predictions in purple-crowned fairy-wrens	Supported?
Dynamic risk assessment	fitness costs are lower, e.g., lower risk of injury or mortality <sup>a,b</sup>	1. Less risk-taking when greater risk of injury	Yes (Figure 1; Table 2)
Parental investment	brood survival yields greater fitness benefits (greater brood value) <sup>a,c</sup>	2. a. Defense increases with brood size b. Defense increases with brood age (nest stage)	No <sup>d</sup> (Table 2) Yes <sup>e</sup> (Table 2)
		3. Breeders defend more than helpers (reflecting higher average relatedness to brood)	Yes (Figures 1 and 2; Table 2)
Social group benefits	greater fitness benefits are associated with group members' survival (e.g., through group augmentation, reciprocity, parental nepotism, and obtaining a mate/breeding position)	4. Male helpers defend more than female helpers 5. Helpers defend more when threat to adult group members	Yes (Figure 2) Yes (Figure 1)

<sup>a</sup>Montgomerie and Weatherhead 1988

<sup>b</sup>Dugatkin and Godin 1992

<sup>c</sup>Trivers 1972

<sup>d</sup>Variation in brood size was limited (mean  $\pm$  SD =  $3 \pm 0.8$ , range = 2–5), potentially contributing to the lack of detection of an effect.

<sup>e</sup>Likelihood of defense overall increased with brood age, whereas the intensity of defense increased with brood age for helpers only.

Most breeding takes place during the monsoonal wet season (December–March) (Rowley and Russell 1993; Kingma et al. 2010). Only the breeder female builds the nest and incubates eggs. For the current experimental study, we followed 50 groups between December 2016 and May 2017, recording group size and social status (breeder and helper) of each group member during regular visits (at least once per week). Breeder females were followed closely for signs of breeding. All nests found were checked regularly to determine the laying date, clutch size, hatch date, and the number of nestlings. Clutch size ranges from one to five eggs (mean  $\pm$  SE =  $3 \pm 0.03$ ), the incubation period lasts for around 14 days and the nestling period for 13 days (Kingma et al. 2010; personal observations). Only 22% of nests with eggs produce at least one fledgling, with nest predation being the main source of nest failure (57% of 685 nests; Hidalgo Aranzamendi 2017; Hidalgo Aranzamendi et al. 2019). Common nest predators at our study site include varanid lizards (goannas; e.g., *Varanus mitchelli* and *Varanus mertensi*; 61% of predation events), avian predators (e.g., *Centropus phasianinus* and *Dacelo leachii*; 16% of predation events), and snakes (e.g., *Antaresia childreni* and *Boiga irregularis*; 10% of predation events; based on 31 predation events captured on camera; Teunissen et al. unpublished data).

## Experimental methods

We quantified individual contribution to predator defense in response to models representing 1) a nest predator (Merten's water monitor, *V. mertensi*), 2) a predator of nests and adults (brown goshawk, *Accipiter fasciatus*), 3) a brood parasite (shining bronze-cuckoo, *Chrysococcyx lucidus*), and 4) a control model presenting no threat (peaceful dove, *Geopelia placida*; see below). Experiments were conducted between 7 February and 24 April 2017, during the (early) incubation stage ( $N = 29$  experiments, mean number of days since last egg laid at first trial  $\pm$  SE =  $3.3 \pm 0.4$ ; range = 1–11 days) and during the nestling stage ( $N = 22$  experiments, mean number of days posthatching at first trial  $\pm$  SE =  $6.3 \pm 0.1$ ; range = 5–7 days), adding up to a total of 51 experiments (i.e., 204 trials; all four models were presented for each experiment) at 37 nests in 33 fairy-wren territories (group size ranged from 2 to 7, mean  $\pm$  SE =  $3.3 \pm 0.2$ ). Responses were recorded for 37 helpers (24 males and 13 females) and 67 breeders

(34 males and 33 females). At 14 nests, experiments were conducted twice—once during the egg stage and again during the nestling stage. Nestling banding always took place after the final trial had been concluded to minimize carryover effects of disturbance at the nest on antipredator responses during the experiment.

For each experiment, we placed, in turn, four models near the nest (see Supplementary Figure S1a,c):

- 1) Goanna: a plastic model of approximately 50 cm length (head to tail) representing a juvenile Merten's water monitor in standing posture. The model was painted based on photos of natural specimens, and we used reflectance spectra and psychophysical models of avian vision (Delhey et al. 2015) to confirm that the painted model displayed natural colors (data available upon request). Water monitors (*V. mertensi* and *V. mitchelli*) of this size are predators of both eggs and nestlings but pose very little threat to adult fairy-wrens.
- 2) Goshawk: a taxidermied brown goshawk (size 40–50 cm; Pizzey and Knight 2012) mounted in a natural perched posture on a short stick. This species is a predator of both nests and adult fairy-wrens.
- 3) Cuckoo: a taxidermied shining bronze-cuckoo (size 16–18 cm; Pizzey and Knight 2012) mounted in a natural perched posture on a short stick. Although this species does not occur at our study site, it is morphologically similar to the Horsfield's bronze-cuckoo (*Choreutis basalis*), which occasionally parasitizes purple-crowned fairy-wren nests (Langmore et al. 2011), and mobbing responses of other fairy-wrens to both cuckoo species are equivalent (Payne et al. 1985). Bronze-cuckoos pose a threat to the nest at all stages; during the laying and early incubation stage, they may parasitize fairy-wren nests, resulting in the fairy-wren eggs and/or nestlings being ejected from the nest by the cuckoo nestling and, although rare, bronze-cuckoos can also depredate the nest (Guppy et al. 2017). The reproductive costs associated with successful parasitism by a cuckoo are greater than those associated with nest predation alone as it involves loss of the brood and extended costly parental care provided to young cuckoos (Rothstein 1990; Feeney et al. 2012). However, cuckoos do not depredate adults.

- 4) Control: a taxidermied peaceful dove (a nonthreatening species) mounted in a natural perched posture on a short stick. Peaceful doves are a common species at our study site that are similar in size to shining bronze-cuckoos (19–21 cm vs. 16–18 cm; Pizzey and Knight 2012) and pose no threat to fairy-wren nests or adults.

Two exemplars of each model type were used and switched between trials to control for potential model effects. For each experiment, one exemplar of each model type was presented with two presentations per day over 2 days. Models were presented in a different order each time in a balanced design of presentation sequences to account for any possible order effects. All trials took place between 5:30 AM and 1:00 PM during calm, dry weather. During experiments, the stick supporting each taxidermied mount was fitted inside a 25- × 25- × 60-cm cage constructed from mist net tightly strung around a wooden frame (see [Supplementary Figure S1b](#)) to protect mounts from damage by fairy-wren attacks (although physical attacks were rare, the net did not seem to present a visual barrier because some individuals touched the net more than once; no birds got entangled). The cage was either suspended from a nearby branch or, in few cases, placed on the ground, so the model was at nest height (range = 0.2 to 3.3 m high). The cage was placed approximately 1 m from the nest (mean  $\pm$  SE =  $1.2 \pm 0.03$  m). The goanna model was not placed in the cage but, instead, placed approximately 20 cm from the nest on a branch or Pandanus leaf (mean  $\pm$  SE =  $21 \pm 0.5$  cm), facing the nest entrance, and attached to the vegetation with black wire (see [Supplementary Figure S1d](#)). These different ways of presenting the models represent how avian and reptilian predators, respectively, naturally approach a fairy-wren nest, with their respective differences in mobility resulting in a similar immediate risk to the nest ([Montgomerie and Weatherhead 1988](#)).

Prior to the first trial of the day, the empty cage was placed, as well as a camouflage hide set up approximately 10 m from the nest, providing a clear view of the nest and its surrounding area. Both were left for at least 30 min before the start of the first trial to allow the birds to get accustomed. When none of the birds in the group were within visible distance of the nest, the model was placed. The trial commenced as soon as at least one individual fairy-wren approached to within 2 m of the model or started producing alarm calls and continued for 10 min. One observer (N.T.) dictated the behavioral responses of each bird in the focal group on a voice recorder. For larger groups ( $\geq 5$  individuals;  $N = 7$  nests), a second observer was present to additionally record the behavioral responses of all group members; this confirmed that the first observer had not missed any of the birds' responses. At the end of the trial, the model was removed, and the next model was presented after an interval of at least 90 min.

Individuals were considered to respond to the model if they produced alarm calls, approached to  $< 2$  m of the model but without going to the nest to incubate, feed, or brood and/or stayed within 2–5 m but intently focused on the model (often while exhibiting freezing behavior; see, e.g., [Cresswell et al. 2009](#); [Cunningham and Magrath 2017](#)). Thus, birds exhibiting normal nest attendance behavior or simply foraging near the nest by chance were never considered to respond to the model; approaches to the nest were only counted as a predator defense response if birds that were carrying food aborted their nest visit and directed their attention to the model or if they were directly approaching the predator itself rather than the nest. Predator defense was quantified as five measures

of defense behavior: 1) likelihood of response (as defined above), 2) nearest distance to the model, 3) time spent  $< 2$  m and 4)  $< 0.5$  m of the model (only including time spent near the model as part of predator defense behavior, not as part of normal nest attendance behavior; see criteria of response described above), and (5) number of alarm calls produced during each trial. These included the very common typical fairy-wren alarm calls—or mobbing calls ([Feeney et al. 2013](#))—and aerial alarm calls often produced in response to aerial predators overhead (personal observations); we did not include whining calls ([Langmore et al. 2012](#); [Feeney and Langmore 2013](#)) in this analysis because these are generally given at a high rate by multiple individuals and can, therefore, not be quantified accurately during observations or attributed to individuals. From audio recordings of a subset of trials encompassing 12 477 alarm calls, whining calls made up only 6% of all alarm calls, whereas mobbing calls constituted 90% of recorded alarm calls. Physical attacks only occurred in two trials and could, therefore, not be analyzed separately.

### Statistical analyses

All analyses were performed in R 3.4.4 ([R Core Team 2018](#)). In 89% of 153 predator model trials, at least one individual in the group exhibited defense behavior in response to the model presented, whereas individuals responded to the control model in only 8% of trials and, indeed, overall, individuals were highly more likely to engage in nest defense to any of the predator models compared with the control (generalized linear model [GLM]:  $\beta \pm \text{SE} = 2.67 \pm 0.41$ ,  $z = 6.51$ ,  $P < 0.01$ ;  $\beta \pm \text{SE} = 3.00 \pm 0.41$ ,  $z = 7.38$ ,  $P < 0.01$ ; and  $\beta \pm \text{SE} = 3.27 \pm 0.41$ ,  $z = 7.98$ ,  $P < 0.01$  for the cuckoo, goanna, and goshawk model, respectively). Control model presentations were, therefore, excluded from any further statistical analyses. Cases where the focal bird might not have been able to detect the model (i.e., where the bird was not seen at all during the trial and its group members did not give any alarm calls that may have alerted it to the presence of the model) were excluded from analyses ( $N = 71$  of 498). In all trials, at least one individual in the group was able to detect the model. Only one group contained a juvenile ( $< 145$ -days old) at the time of the experiment; this bird was excluded from analyses because juveniles generally do not help ([Kingma et al. 2010, 2011](#)).

We constructed five sets of statistical models to quantify how each of the five defense behaviors described above varied between breeders and helpers in response to predators of varying threat, and with brood value, to test predictions as outlined in [Table 1](#). We included as explanatory variables: predator type (goanna, goshawk, and cuckoo; prediction 1 in [Table 1](#)), brood size (prediction 2a), nest stage (eggs and nestlings; prediction 2b), status (breeder and helper; prediction 3), sex (male and female), the interaction between status and sex (prediction 4), and the interaction between status and predator type (prediction 5). We also included the interaction between status and nest stage to test the possibility that helpers and breeders respond differently to changes in brood value and the interaction between nest stage and predator type because we expect birds to respond more strongly to cuckoos during the early egg stage in particular, when the risk for brood parasitism is highest. Additionally, we included group size as a covariate to control for potential load-lightening effects (e.g., [Johnstone 2011](#); [van Boheemen et al. 2019](#)) and trial number (1–4) to control for order effects. Because experiments were conducted twice at 14 nests (i.e., we had 14 “second” experiments, all at the nestling stage, and 37 “first” experiments: 24



at the egg stage and 13 at the nestling stage), we included experiment number (first and second) as an additional factor in the model. Experiment number did not have a significant effect on any of the response measures analyzed (Supplementary Table S1), and analyses yielded overall similar results. However, nonindependence of nest stage and experiment number likely resulted in a nonsignificant main effect of nest stage on the likelihood of response; therefore, we did not include experiment number in final statistical models presented here. Although individuals <1-year old provision nestlings less and may, therefore, be expected to also defend less against predators (Kingma et al. 2011), we did not include focal individual age in our models because nearly all (99%) breeders compared with 78% of helpers in our data set were older than 1 year. All models included bird ID, nest ID, and exemplar (nested within predator type) as random effects. To analyze the likelihood of response, a generalized linear mixed model (GLMM) with binomial distribution was built using the packages “lme4” (Bates et al. 2015) and “lmerTest” (Kuznetsova et al. 2017). The nearest distance that the focal bird approached the model ( $[\log+1]$ -transformed to meet assumptions of normality) was analyzed using a linear mixed model (LMM), including only birds that responded. Post hoc tests were performed using the “glht” function from the “multcomp” package (Hothorn et al. 2008), controlling for any interaction effects. Because individuals often did not produce alarm calls (72% of trials), spent no time <2 m (63%) or <0.5 m of the model (92%), these response variables were analyzed with a Bayesian GLMM with a negative binomial distribution using the “rstanarm” package (Goodrich et al. 2018). Priors were set to a normal distribution with mean = 0 and variance = 10, and variance = 100 for the intercept prior. Three chains were run, of 15 000 iterations, with a thinning interval of 20 and a warm-up period of 5000. Visual inspection of the trace, density, and autocorrelation plots of the parameters using the “rstan” package (Stan Development Team 2018) confirmed convergence of the model and showed no sign of autocorrelation. We present posterior means and 95% credible intervals (CI). Using GLMMs with binomial distribution instead (analyzing presence/absence of alarm calls, approach <2 and <0.5 m) yielded qualitatively similar results for all three variables.

## RESULTS

### Defense behavior and risk

Overall, individual fairy-wrens adjusted their defense response to the threat posed by the predator regardless of social status. First, birds were marginally more likely to respond to goshawk models (70% of trials) compared with cuckoo models (56% of trials; Tukey's honest significant difference [HSD]:  $\beta \pm \text{SE} = 0.94 \pm 0.43$ ,  $z = 2.21$ ,  $P = 0.07$ ), with no difference in likelihood of response toward goanna (64% of trials) and cuckoo ( $\beta \pm \text{SE} = 0.51 \pm 0.43$ ,  $z = 1.18$ ,  $P = 0.46$ ) or goanna and goshawk models ( $\beta \pm \text{SE} = -0.44 \pm 0.42$ ,  $z = -1.03$ ,  $P = 0.56$ ; Figure 1a). Second, the physical response differed between predator types; birds approached both goanna and cuckoo models to a closer distance than goshawk models (Tukey's HSD:  $\beta \pm \text{SE} = -0.32 \pm 0.06$ ,  $z = -5.54$ ,  $P < 0.01$ , and  $\beta \pm \text{SE} = -0.23 \pm 0.06$ ,  $z = -3.58$ ,  $P < 0.01$ , respectively), with no difference between goanna and cuckoo models ( $\beta \pm \text{SE} = -0.09 \pm 0.07$ ,  $z = -1.27$ ,  $P = 0.41$ ; Figure 1b). Furthermore, individuals spent more time within 2 m of goanna models (Table 2; Figure 1c) and never came within 0.5 m of the goshawk, although they did get this close to goannas and cuckoos (Table 2). Physical

attacks of the model were rare; one bird attacked a goanna model twice and another a cuckoo model twice; the goshawk was never physically attacked. The acoustic response (number of alarm calls produced) did not differ between predator types (Table 2; Figure 1d). We found no significant interaction effect of predator type and nest stage for any of the response parameters (Table 2).

### Defense behavior and social status

Breeders showed greater investment in nest defense than helpers: helpers were considerably less likely to respond (40% of trials compared with 59% for breeders; GLMM:  $P < 0.01$ ; Table 2; Figures 1a and 2a); did, on average, not approach as close to the predator model (LMM:  $P = 0.02$ ; Table 2; Figures 1b and 2b); spent less time within 2 m of the model (Table 2; Figures 1c and 2c) and within 0.5 m of the model (Table 2); and produced fewer alarm calls (Table 2; Figures 1d and 2d).

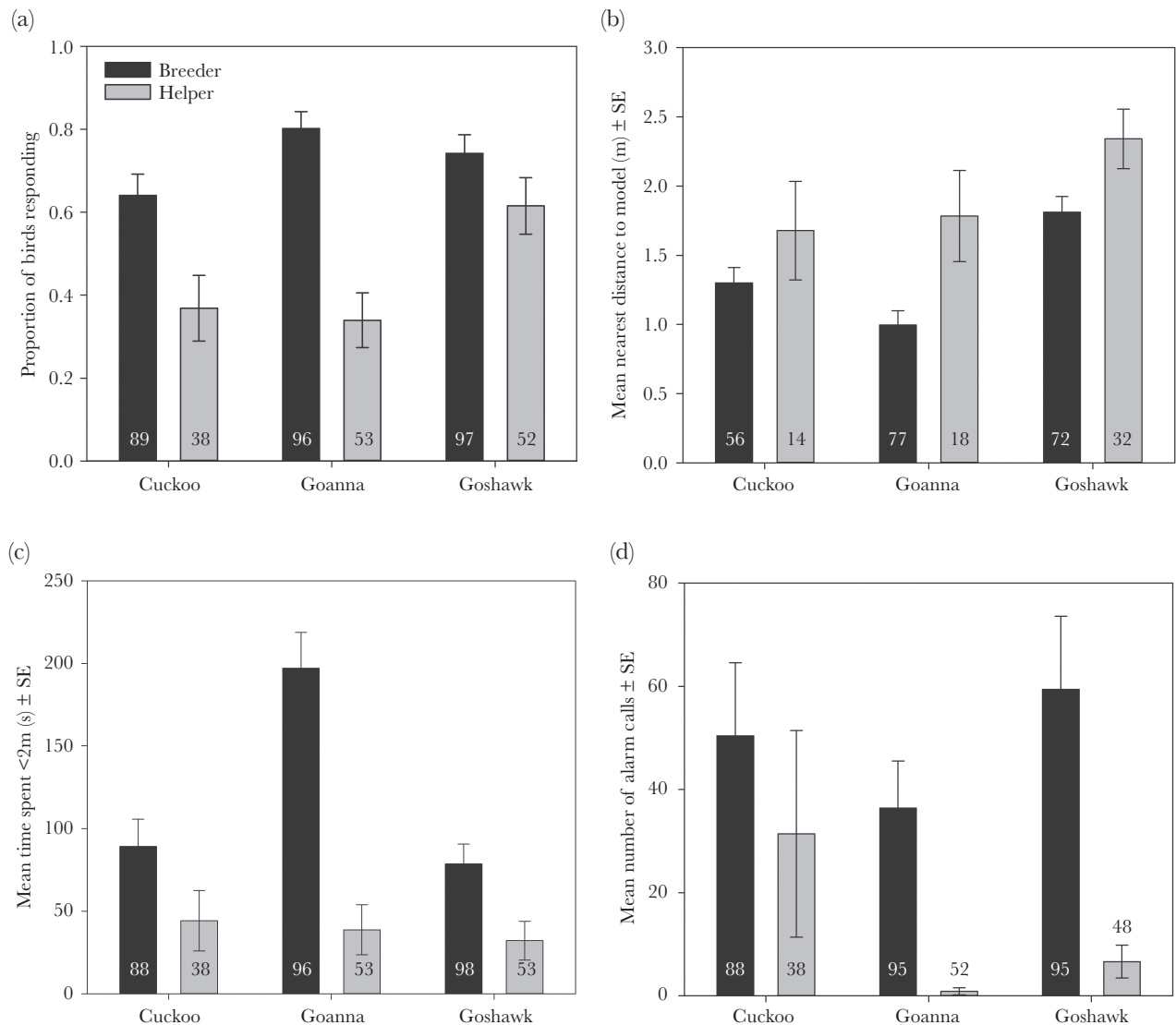
Among breeders, females generally showed stronger defense responses than males, whereas male helpers defended more strongly than female helpers (significant interaction effect of status and sex on the likelihood of response, time spent <2 m, and the number of alarm calls; Table 2; Figure 2). Generally, males produced fewer alarm calls compared with females, independent of social status (Table 2; Figure 2d).

Breeders and helpers responded to the type of predator differently; helpers were more likely to respond to the goshawk compared with goanna and cuckoo models, whereas breeders were about equally likely to respond to all three types of predators (interaction term:  $P = 0.02$ ; Table 2; Figure 1a). Helpers also produced fewer alarm calls in response to goanna models in particular, whereas breeders produced equal numbers of alarm calls to all models (Table 2; Figure 1d).

Individuals were more likely to respond to the predator during the nestling stage, when brood value is higher, compared with during the egg stage (Tukey's HSD:  $\beta \pm \text{SE} = 0.59 \pm 0.28$ ,  $z = 2.12$ ,  $P = 0.03$ ). However, although the likelihood of response increased to a similar degree for breeders and helpers, they differed in how they adjusted the intensity of their response according to nest stage: during the nestling stage, helpers spent significantly more time <0.5 m of the model than during the egg stage and produced more alarm calls (Table 2), whereas breeders showed no difference in the intensity of response between nest stages. Neither breeders nor helpers adjusted their response with brood size (Table 2).

## DISCUSSION

We provide, as far as we are aware, the first simultaneous test of the dynamic risk assessment and parental investment theories for predator defense behavior in a cooperatively breeding bird species. Based on these theories, we predicted individuals to modify defense behavior with the risk of injury and brood value and predicted that breeders in this cooperative fairy-wren should defend more than helpers. Additionally, we proposed that, in cooperative breeders, predator defense behavior should also be influenced by current and future social fitness benefits from adult group members surviving and predicted that male helpers should, therefore, defend more than female helpers and that helpers prioritize defense toward a predator of adults rather than the brood (see Table 1). Our results show that variation in defense behavior can be explained by each of these theories as we discuss below.



**Figure 1**

Responses by breeders (black bars) and helpers (gray bars) to each predator type, measured as (a) likelihood of response, (b) nearest distance to model, (c) time spent <2 m of the model, and (d) number of alarm calls produced. Breeders defended more strongly than helpers overall, and responses differed with predator type (in interaction with social status for (a) and (d)). Values are based on raw data and results of statistical analyses are provided in Table 2. Numbers in bars indicate sample sizes. Sample sizes differ between predator types and response measures because only cases where birds were able to detect the model are included, and response measures could in a few instances not accurately be quantified. For nearest distance to the model (b), data are presented for individuals that responded only.

### Dynamic risk assessment: defense behavior and risk of injury

The key prediction of the dynamic risk assessment hypothesis that individuals modulate their response according to the level of threat and alter their behavior to minimize personal risk (Montgomerie and Weatherhead 1988; Dugatkin and Godin 1992) was clearly supported (Table 1). Both breeders and helpers changed their behavior according to the level of individual risk represented by the models, keeping a greater distance from goshawk models—a predator that is associated with greater risk of injury for adults—compared with goanna and cuckoo models—predators that pose very little risk to adults. The lack of response to control models in comparison indicates that goanna and cuckoo models were

nonetheless perceived as a threat to the nest. Our findings suggest that fairy-wrens are able to distinguish between predator types and modify their defense behavior according to the degree of risk (as in Campobello and Sealy 2010), although it should be noted that goshawk models may also present a greater size stimulus compared with cuckoo and control models. Individual fairy-wrens in our study did not adjust the frequency of alarm calls according to the threat posed by the predator. This highlights the need to incorporate not only the commonly studied acoustic response (as in, e.g., Edelaar and Wright 2006; Graw and Manser 2007; Griesser 2009; Colombelli-Negrel et al. 2010a, 2010b; Feeney et al. 2013) but also the physical response when testing predictions from risk assessment theory as individuals may change defense strategy

**Table 2**

The effect of a number of factors on five measures of predator defense behavior by individuals: 1) likelihood of response ( $N = 427$  individual trials), 2) nearest distance to model ( $N = 270$ ), 3) time spent  $< 2$  m of the model ( $N = 426$ ), 4) time spent  $< 0.5$  m of the model ( $N = 427$ ), and 5) number of alarm calls produced ( $N = 416$ ). Effect size, SE, and  $P$ -values are given where frequentist statistical models were used and the effect size and 95% confidence interval (CI) where Bayesian methods were used. For the main effects of variables that are also included in interaction terms,  $P$ -values presented were obtained through Tukey's HSD post hoc analyses controlling for interaction effects. Significant terms are highlighted in bold

	Likelihood to respond		Log (nearest distance to model)*		Time spent $< 2$ m		Time spent $< 0.5$ m		Number of alarm calls	
	Effect size ( $\pm$ SE)	$P$	Effect size ( $\pm$ SE)	$P$	Effect size (95% CI)		Effect size (95% CI)		Effect size (95% CI)	
Intercept <sup>a</sup>	1.55 $\pm$ 0.87	0.07	<b>0.72 <math>\pm</math> 0.16</b>	<b>&lt;0.01</b>	<b>4.9 (2.9, 6.8)</b>		-0.5 (-6.7, 5.0)		<b>3.3 (0.9, 5.6)</b>	
Status <sup>b</sup>	<b>-2.40 <math>\pm</math> 0.72</b>	<b>&lt;0.01</b>	<b>0.17 <math>\pm</math> 0.15</b>	<b>0.02</b>	<b>-3.0 (-4.5, -1.0)</b>		<b>-6.7 (-12.9, -1.4)</b>		<b>-7.2 (-10.5, -4.2)</b>	
Sex <sup>c</sup>	-1.15 $\pm$ 0.39	0.53	0.17 $\pm$ 0.06	0.23	-0.6 (-1.5, 0.1)		-1.4 (-4.0, 0.8)		<b>-1.3 (-2.3, -0.3)</b>	
Brood size	0.01 $\pm$ 0.21	0.95	0.01 $\pm$ 0.04	0.90	0.1 (-0.4, 0.5)		0.1 (-1.1, 1.7)		0.2 (-0.5, 0.8)	
Predator type (goanna) <sup>d</sup>	1.26 $\pm$ 0.56	0.46	-0.13 $\pm$ 0.07	0.41	<b>1.2 (0.0, 2.4)</b>		2.2 (-0.1, 5.1)		-0.3 (-1.8, 1.0)	
Predator type (goshawk) <sup>d</sup>	0.78 $\pm$ 0.53	0.07	<b>0.20 <math>\pm</math> 0.08</b>	<b>&lt;0.01</b>	0.4 (-0.9, 1.7)		<b>-14.1 (-27.2, -5.7)</b>		0.8 (-0.8, 2.4)	
Nest stage <sup>e</sup>	<b>0.46 <math>\pm</math> 0.48</b>	<b>0.03</b>	0.05 $\pm$ 0.09	0.68	0.8 (-0.5, 2.3)		-0.5 (-2.9, 2.9)		0.9 (-0.8, 2.6)	
Group size	<b>-0.22 <math>\pm</math> 0.11</b>	<b>0.049</b>	0.03 $\pm$ 0.02	0.31	<b>-0.3 (-0.5, -0.1)</b>		0.2 (-0.5, 1.0)		-0.1 (-0.4, 0.2)	
Trial	0.04 $\pm$ 0.11	0.74	<b>-0.05 <math>\pm</math> 0.02</b>	<b>0.01</b>	0.1 (-0.1, 0.4)		0.7 (-0.1, 1.6)		0.3 (-0.1, 0.7)	
Status (helper) $\times$ Sex (male)	<b>1.89 <math>\pm</math> 0.67</b>	<b>&lt;0.01</b>	-0.18 $\pm$ 0.13	0.17	<b>2.2 (0.7, 3.9)</b>		3.6 (-0.9, 8.8)		<b>3.9 (1.6, 6.3)</b>	
Status (helper) $\times$ Predator type (goanna)	<b>-1.08 <math>\pm</math> 0.64</b>	<b>0.02</b>	0.24 $\pm$ 0.14	0.19	-0.3 (-2.2, 1.3)		-1.3 (-6.9, 4.2)		<b>-2.7 (-5.3, 0.0)</b>	
Status (helper) $\times$ Predator type (goshawk)	<b>0.62 <math>\pm</math> 0.63</b>	<b>0.02</b>	0.08 $\pm$ 0.13	0.19	0.1 (-2.2, 1.9)		-2.9 (-19.0, 12.3)		0.9 (-1.8, 3.8)	
Status (helper) $\times$ Nest stage (nestlings)	0.74 $\pm$ 0.53	0.17	-0.05 $\pm$ 0.11	0.66	1.1 (-0.5, 2.7)		<b>5.2 (0.6, 10.5)</b>		<b>4.4 (2.1, 7.0)</b>	
Nest stage (nestlings) $\times$ Predator type (goanna)	-0.43 $\pm$ 0.61		-0.14 $\pm$ 0.11	0.28	-0.5 (-2.4, 1.2)		1.4 (-2.9, 6.2)		-0.4 (-2.8, 2.0)	
Nest stage (nestlings) $\times$ Predator type (goshawk)	-0.28 $\pm$ 0.59	0.74	-0.01 $\pm$ 0.11		-0.9 (-2.8, 0.8)		-4.8 (-21.3, 9.3)		-1.5 (-3.7, 0.6)	

<sup>a</sup>Reference category overall is female breeder; cuckoo model; egg stage.

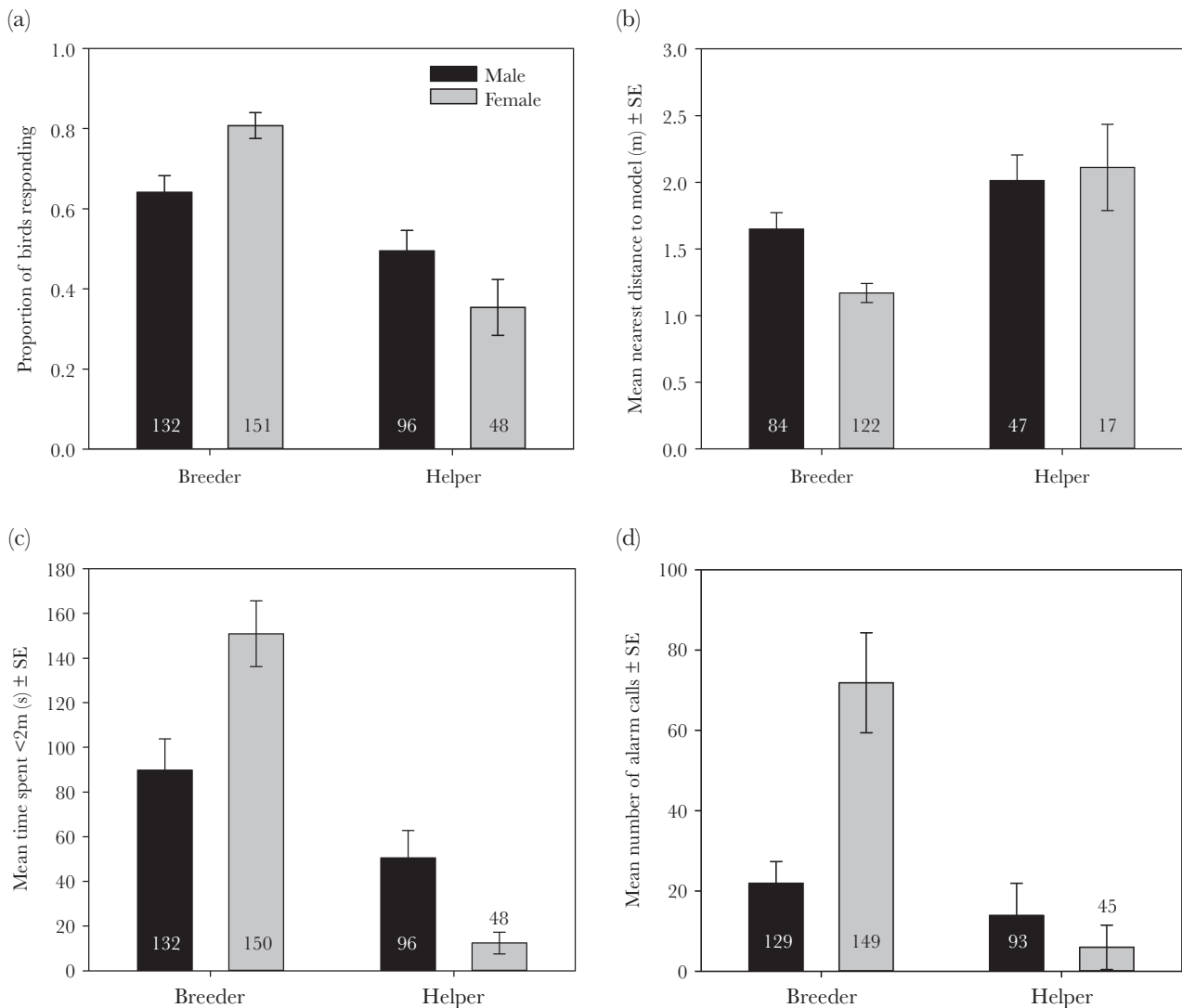
<sup>b</sup>Helper compared with reference category breeder.

<sup>c</sup>Male compared with reference category female.

<sup>d</sup>Compared with reference category cuckoo model.

<sup>e</sup>Nestling stage compared with reference category egg stage.

\*Only includes individuals that responded to the model.



**Figure 2**

Responses by male (black bars) and female (gray bars) breeders and helpers to all predator types combined, measured as (a) likelihood of response, (b) nearest distance to model, (c) time spent <2 m of the model, and (d) number of alarm calls produced. Breeders defended more strongly than helpers overall and, among breeders, females responded more strongly than males, whereas, among helpers, males responded more strongly than females (a, c, d). Values are based on raw data and results of statistical analyses are provided in Table 2. Numbers in bars indicate sample sizes. For nearest distance to the model (b), data are presented for individuals that responded only.

rather than intensity (Swaigood et al. 1999; Strnad et al. 2012; Koberoff et al. 2013).

Although goanna models were placed closer to the nest compared with goshawk and cuckoo models and predator defense intensity has been found to decrease with predator distance from the nest in other species (Kleindorfer et al. 2005; Colombelli-Negrel et al. 2010b), this is unlikely to have confounded our results. A goanna at 20 cm from the nest is expected to represent a similar level of threat to the nest as a goshawk or cuckoo at 1 m from the nest because avian predators have higher mobility (discussed in detail in Montgomerie and Weatherhead 1988). In addition, the closest approach and time spent within 0.5 m of the model did not differ between cuckoos and goannas, despite their difference in distance from the nest, suggesting that differences in physical response to the goshawk indeed reflect a greater perceived threat to adults compared with a threat to the nest only for goannas and cuckoos.

Our expectation that the response to cuckoos should be stronger than to other nest predators, and particularly during the early egg stage (Feeney et al. 2013), was not supported. We expected this because cuckoos are associated with greater reproductive costs than other nest predators due to the risk of extended periods of care for the offspring of brood parasites (Rothstein 1990; Feeney et al. 2012). However, we found no interacting effect of predator type and nest stage on nest defense and, overall, fairy-wrens defended less often against cuckoos than against goshawks. This is in contrast to previous studies reporting a stronger response to brood parasites and, indeed, nest predators more generally during the nest stage where the associated threat is greatest (e.g., early egg stage for brood parasites and nestling stage for predators of nestlings; Patterson et al. 1980; Burgham and Picman 1989; Campobello and Sealy 2010). Possibly, not all individuals in our study area were familiar with cuckoos as



a result of relatively low brood parasitism rates at our study site (Langmore et al. 2012); brood parasitism of purple-crowned fairy-wren nests occurred in 4 of 9 years (2005–2010 and 2015–2017), with a mean  $\pm$  standard deviation [SD] of  $4.4 \pm 4.5\%$  (maximum = 11%) of nests parasitized in years where at least some cuckoos hatched in fairy-wren nests. Because cuckoo recognition may require learning (Langmore et al. 2012; Feeney and Langmore 2013), unfamiliar individuals may respond less strongly, but we currently have insufficient data to test this idea.

### Parental investment: defense behavior and brood value

Parental investment theory predicts that individuals increase nest defense intensity with increasing brood value (relatedness, age, or size of the brood; Trivers 1972; Montgomerie and Weatherhead 1988). These predictions were largely confirmed.

Although future analyses will possibly enable us to reveal a direct relationship between variation in relatedness and individual defense behavior, our observed greater investment in predator defense by breeders compared with helpers is in agreement with the prediction that relatedness affects defense (Table 1). Breeders on average have a higher genetic stake in the current brood compared with helpers: given near monogamy in this species (Kingma et al. 2009), both breeders are full parents of the brood, whereas helpers are, on average, less related due to breeder turnover and dispersal (Kingma et al. 2010, 2011). Dynamic risk assessment theory may provide an alternative explanation, predicting that nest defense intensity increases when there are fewer opportunities for future reproduction. Breeders may invest more in current relative to future reproduction and, therefore, experience a lower cost of lost future reproduction and defend more intensely compared with helpers. However, to explore this possibility fully, we will first need to gain a better understanding of future prospects for reproduction for both breeders and helpers. It is worth noting that our finding that breeders defend more is unlikely to simply reflect breeders having higher probability to detect or be in the vicinity of the model because they attend the nest more often than helpers (Kingma et al. 2010, 2011): only individuals that were able to detect the model were included in the analyses, and only birds that showed a response to the model were considered to engage in predator defense behavior.

Studies on noncooperatively breeding species have generally reported increased defense of older and larger broods (e.g., Patterson et al. 1980; Thornhill 1989; Lavery and Colgan 1991; Amat et al. 1996; Olendorf and Robinson 2000; Rytönen 2002; Svagelj et al. 2012; but see Grim 2005; Campobello and Sealy 2010). We found support for increased defense for older broods, with both breeders and helpers defending more often at later nest stages (Table 1). Contrary to parental investment theory, however, defense behavior did not vary with brood size, possibly because variation in clutch size is relatively small (mean  $\pm$  SD =  $3 \pm 0.8$  for nests included in the current study; Table 1). Moreover, previous studies on nest defense in cooperatively breeding birds have reported no effect of size or age of the brood (Arnold 2000) or a stronger response for older broods (van Asten et al. 2016), but these studies did not test for differences between helpers and breeders at different nest stages. Although both breeders and helpers were more likely to defend in later nest stages, we found that the intensity of defense only increased for helpers and not for breeders. The latter might be a

saturation effect because breeder defense is always high, whereas helpers may be more sensitive to changes in brood value than breeders.

### Social benefits: social status and helper benefits

Breeders and helpers differed in how they modulated their response to predators of varying threat (interaction effect of social status and predator type), with helpers more likely to defend against a predator of adults than against nest predators (Table 1). This is in agreement with predictions based on social benefits: for helpers, adult group members' survival may be more important than the survival of the brood. Helpers may obtain significant benefits from adult group members through parental nepotism (i.e., facilitation of greater access to resources for mature offspring), reciprocal or mutualistic benefits of group augmentation (i.e., greater survival or future reproduction in larger groups due to, e.g., reciprocal actions or safety in numbers), or the presence of potential future mates in the group (i.e., unrelated opposite-sex group members). Hence, adult group members offer benefits that are larger and/or more immediate than young group members (Ekman et al. 2000, 2004; Kokko et al. 2001; Kingma 2017; Teunissen et al. 2018), and their defense provides greater or more immediate payoffs.

Likewise, the observation that, amongst helpers, males defend more intensely than females can be explained by greater social benefits obtained from the survival of the brood and adult group members (Table 1). In *M. coronatus*, male helpers are more likely to stay and have greater chances to inherit a breeding position in the group (Kingma et al. 2011) and, therefore, obtain greater immediate and future group augmentation benefits if the brood, as well as adult group members, survive (Kokko et al. 2001; Margraf and Cockburn 2013; Kingma 2017). Similarly, in cooperative meerkats, *Suricata suricatta*, female helpers (the philopatric sex), but not male helpers, increase vigilance behavior when pups are present (Santema and Clutton-Brock 2013), further supporting the notion that social benefits of predator defense may be closely linked to sex differences in philopatry. Possibly, nest defense by helpers may even serve to advertise quality to particular group members (Montgomerie and Weatherhead 1988; Zahavi 1995): for example, in Arabian babblers, *Turdoides squamiceps*, subordinates mob predators of adults more than breeders, possibly, to advertise their quality for the formation of dispersal coalitions (Maklakov 2002). Future research on *M. coronatus* will investigate if and how predator defense by helpers is aligned with individual benefits of helping and group living in this species and is expected to enhance our understanding of predator defense in cooperative breeders and how helpers may balance contributions to individual and group success.

## CONCLUSIONS

We show that individuals in a facultatively cooperative breeding fairy-wren modify their defense behavior in complex ways when detecting a predator and that this is aligned with relative risks, as well as individual current and future benefits. Importantly, breeders and helpers seem to use different decision rules in predator defense. Whereas breeders seem generally willing to defend the nest and group members—and they do so more intensely—helpers appear more responsive to changes in brood value and the social benefits associated with the survival of adult group members.

## SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by [Teunissen et al. \(2020\)](#).

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