RESEARCH ARTICLE

From ornament to armament or loss of function? Breeding plumage acquisition in a genetically monogamous bird

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Abstract

1. The evolution of conspicuous male traits is thought to be driven by female mate choice or male–male competition. These two mechanisms are often viewed as distinct processes, with most studies focusing on female choice.

2. However, both mechanisms of sexual selection can act simultaneously on the same trait (i.e., dual function) and/or interact in a synergistic or conflicting way. Dual-function traits are commonly assumed to originate through male–male competition before being used in female choice; yet, most studies focusing on such traits could not determine the direction of change, lacking phylogenetic information.

3. We investigated the role of conspicuous male seasonal plumage in male–male competitive interactions in the purple-crowned fairy-wren *Malurus coronatus*, a cooperatively breeding bird. Male breeding plumage in most *Malurus* species is selected by female choice through extra-pair mate choice, but unlike its congeners, *M. coronatus* is genetically monogamous, and females do not seem to choose males based on breeding plumage acquisition.

4. Our study shows that, within groups, subordinate males that were older, and therefore higher-ranked in the queue for breeder position inheritance, produced a more complete breeding plumage. In line with this, subordinate males that were older and/or displayed a more complete breeding plumage were more successful in competitively acquiring a breeder position.

5. A role as a signal of competitive ability was experimentally confirmed by presenting models of males: in breeding colours, these received more aggression from resident breeder males than in nonbreeding colours, but elicited limited response from females, consistent with competitors in breeding plumage being perceived as a bigger threat to the breeder male.

6. The role of the conspicuous breeding plumage in mediating male–male interactions might account for its presence in this genetically monogamous species. As phylogenetic reconstructions suggest a past female choice function in *M. coronatus*, this could represent a sexual trait that shifted functions, or a dual-function trait that lost one function. These evolutionary scenarios imply that intra- and

intersexual functions of ornaments may be gained or lost independently and offer new perspectives in understanding the complex dynamics of sexual selection.

KEYWORDS

evolutionary trait loss, extra-pair paternity, functional shift, male–male competition, monogamy, seasonal breeding plumage, social dominance, trait co-option

1 | INTRODUCTION

The evolution and maintenance of elaborate male traits have traditionally been attributed to sexual selection, which operates through two mechanisms: mate choice and same-sex competition (Andersson, 1994; Darwin, 1871). Indeed, numerous male secondary sexual characters are assumed to serve to attract breeding partners and/or to repel opponents in contests over breeding resources and opportunities (Andersson, 1994; Clutton-Brock, 2007; Darwin, 1871). Such characters may act as signals of male quality, providing choosy females and/or rival males with information related to individual body condition, fighting ability and genetic constitution (Andersson, 2006; Hamilton & Zuk, 1982; Zahavi, 1975). Although both mechanisms of sexual selection are credited with the evolution of extravagant male characters, most research has focused on female mate choice (Jones & Ratterman, 2009; McCullough, Miller & Emlen, 2016). Moreover, many studies have depicted a dichotomous view of these mechanisms, with different underlying genetic processes at play and costs involved (Hurd & Enquist, 2005; Jones & Ratterman, 2009; Lachmann, Szamado & Bergstrom, 2001; McCullough et al., 2016).

Nevertheless, various studies have now established that some traits could be selected by male–male competition as well as female choice (i.e., dual function; Berglund, Bisazza & Pilastro, 1996; Hoi & Griggio, 2008; Tarof, Dunn & Whittingham, 2005). Hereby, both mechanisms can interact in a synergistic or conflicting way through mutual reinforcement or opposing selection (Hunt, Breuker, Sadowski & Moore, 2009; Qvarnström & Forsgren, 1998; Wong & Candolin, 2005). Choice by females and competition between males may operate simultaneously or sequentially within populations; as both mechanisms can differ in strength and form, total sexual selection operating on a trait may differ considerably from that imposed by either choice or competition in isolation (Hunt et al., 2009). Furthermore, due to spatial and temporal environmental heterogeneity, selection through both mechanisms may fluctuate and therefore generate complex dynamics in overall sexual selection (Miller & Svensson, 2014). The vast majority of dual-function traits are assumed to originate through male–male competition, and subsequently be co-opted for use in female choice (Berglund et al., 1996). This assumption rests upon the idea that females exploit signals used in male–male aggressive interactions because the honesty of such traits is constantly tested in these interactions and cannot be faked without incurring substantial costs (Berglund et al., 1996). However, the reverse process—female choice cues co-opted for use

in male contests—may also occur, although very little evidence for this phenomenon exists (but see Morris, Tudor & Dubois, 2007). Because determining the context in which a dual-function trait initially evolved requires studies of both intra- and intersexual selection in closely related species, as well as phylogenetic information, so far only few studies have been able to test this scenario (Borgia & Coleman, 2000; Morris et al., 2007).

Here, we use the purple-crowned fairy-wren *Malurus coronatus* to investigate the respective roles of female choice and male–male competition in shaping the evolutionary trajectory of a conspicuous male trait. Like most other *Malurus*, the species breeds cooperatively, forms long-term social partnerships and displays seasonal plumages, as both breeder and subordinate males moult annually from a dull nonbreeding plumage into a conspicuous breeding plumage (Peters, Kingma & Delhey, 2013). The timing of moult into breeding plumage by male fairy-wrens is viewed as a classic female choice-driven trait: early moult is strongly selected by female choice for extra-pair (EP) mates who dominate fertilisations (Peters et al., 2013; Brouwer et al., 2017; Figure 1). However, EP mating is very limited in *M. coronatus* (<5% of broods) and mostly driven by incest avoidance (Hidalgo Aranzamendi, Hall, Kingma, Sunnucks & Peters, 2016; Kingma, Hall & Peters, 2013; Kingma, Hall, Segelbacher & Peters, 2009), suggesting no role of female EP mate choice in the evolution of male breeding plumage in this species (Figure 1). In addition, there is no apparent reproductive benefit of early moult (Fan et al., 2017) which, based on the most recent phylogeny (Marki et al., 2017), may thus constitute a vestigial sexual trait (Figure 1). Nevertheless, Fan et al. (2017) reported that breeder males moult earlier than subordinates. Because acquiring and retaining a breeder position is critical for male reproductive success, we hypothesise that male–male competition might drive the persistence of the breeding plumage. We use 6 years of data to test whether variation in breeding plumage of subordinate males predicts success in obtaining a breeder position. Second, we performed model presentations to experimentally test whether plumage state of simulated male intruders affects the strength of territorial defence by breeder males.

2 | MATERIALS AND METHODS

2.1 | Study species

We studied a colour-banded population of *M. coronatus* at the Australian Wildlife Conservancy's Mornington Wildlife Sanctuary (17°31′S, 126°6′E; north Western Australia) from July 2005 to
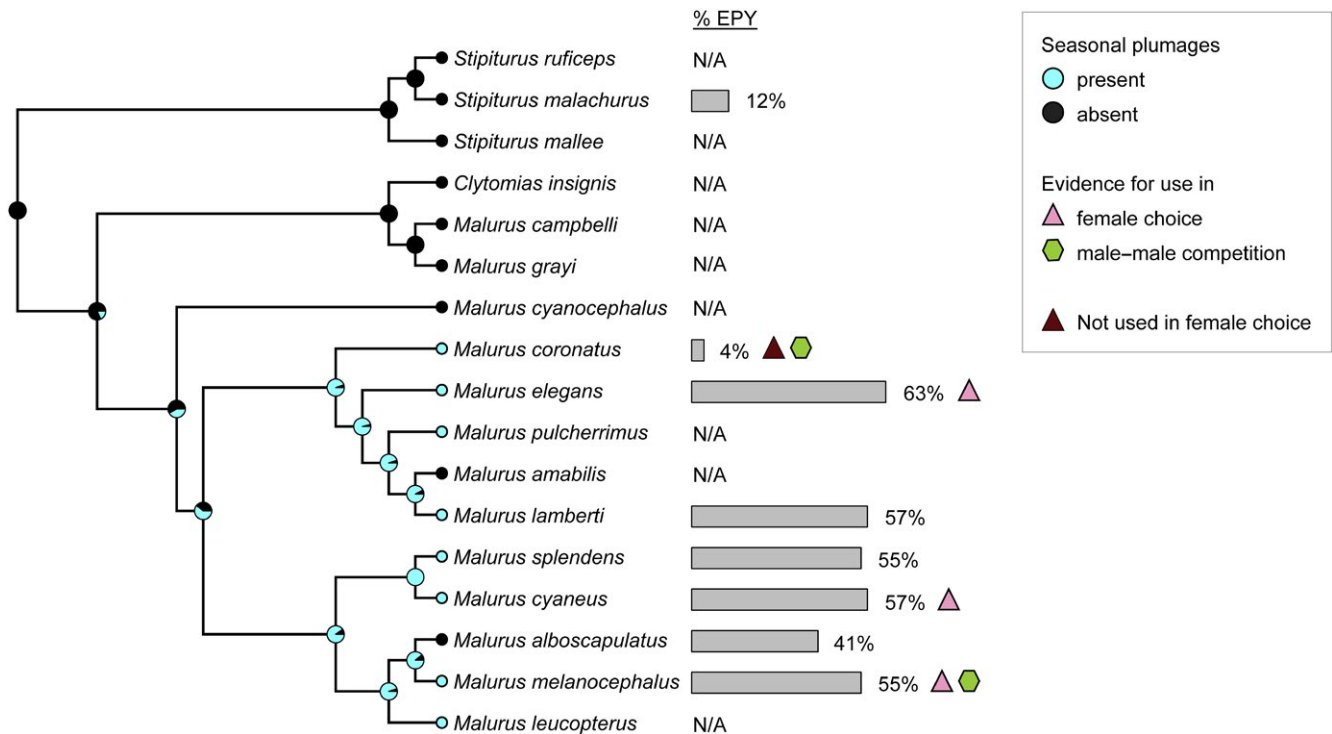
FIGURE 1 Evolution of seasonal plumage in fairy-wrens and emu-wrens. Shown is the ancestral state reconstruction of changes in seasonal plumages for 17 Malurid species, using stochastic mapping (for details see Fan et al., 2017) and based on the supermatrix phylogeny of Marki et al. (2017). Absence of seasonal plumages in *M. amabilis* is based on Schodde (1982). % EPY = levels of extra-pair paternity (proportion of offspring sired by extra-pair males; Brouwer et al., 2017; N/A: no data available) are shown for each species, as well as whether there is evidence that seasonal plumages function in female choice and/or male–male competition (this study; Karubian et al., 2008; Peters et al., 2013; Fan et al., 2017) [Colour figure can be viewed at wileyonlinelibrary.com]

November 2016. These birds are restricted to patchy riparian vegetation of *Pandanus aquaticus* and maintain all-purpose territories year-round, linearly arranged along Annie Creek and the Adcock River (Kingma et al., 2009). *Malurus coronatus* can breed year-round with a peak in breeding activity at this site during the wet season (December–March), and a smaller peak in the late dry season (August-September) in some years (Hall & Peters, 2009; Peters et al., 2013).

Malurus coronatus breeds cooperatively, whereby 40%–70% of dominant breeding pairs (distinguished by duet singing; Hall & Peters, 2008, 2009), are accompanied by a number of nonbreeding male and female subordinates (Kingma, Hall, Arriero & Peters, 2010; Kingma, Hall & Peters, 2011a,b).

Males replace the dull brown nonbreeding head plumage annually with purple-and-black feathers (Peters et al., 2013; Figure 2a,c), and this moult overlaps temporally with breeding in some cases (29% of breeder males; Fan et al., 2017). First-year males and subordinate males complete their moult later than older males and breeder males, respectively (Fan et al., 2017). Moreover, although they usually moult to some degree, only 16% of first-year males develop a complete breeding plumage, whereas most older males do so (Fan et al., 2017; see also results).

Subordinate individuals may acquire a breeder position either by taking over part of the natal territory or establishing a new territory

(*n* = 65), or by filling a vacancy left by a deceased breeder (either inheritance of the home territory or dispersal to another, mostly limited to neighbouring territories—Kingma et al., 2011b; Hidalgo Aranzamendi et al., 2016; *n* = 96). Males less commonly (*n* = 23) take over a territory of a breeder male that has dispersed after divorce or death of the breeder female, and we have no evidence for eviction of the former breeder in such cases. Dispersal to settle as a subordinate elsewhere is relatively uncommon (*n* = 24 of 163 records of subordinate male dispersal).

2.2 | Field methods

From July 2005 to March 2011, weekly population censuses were conducted year-round (01 July = start of austral year) to document group size and social status of each uniquely colour-banded male. From October 2011 to November 2016, this information was recorded biannually in population censuses in October-November and May-June (for details see Hidalgo Aranzamendi et al., 2016; Fan et al., 2017). At each sighting, each observer scored the extent of breeding plumage on a scale between 0% and 100% in 5% increments; finer scores could be assigned when birds were captured. Parentage of local birds was determined using six or nine microsatellite loci (for details see Kingma et al., 2009; Hidalgo Aranzamendi et al., 2016). In addition, throughout the study, birds were routinely
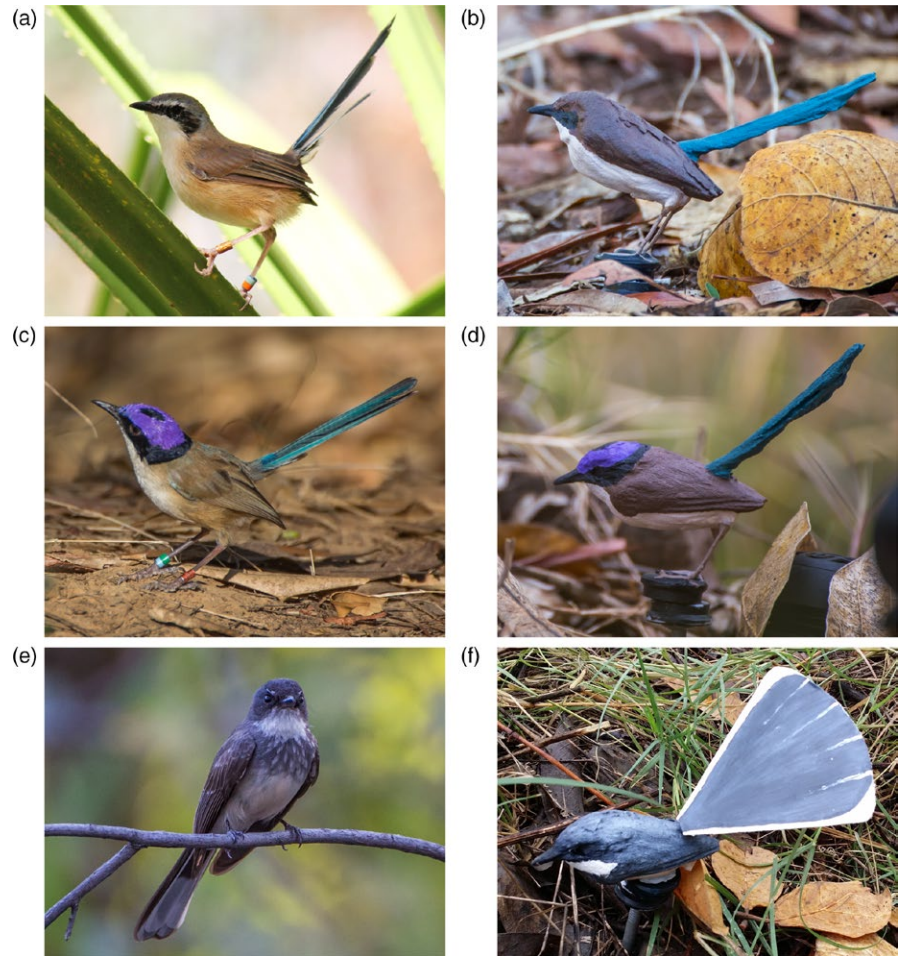
FIGURE 2 Nonbreeding and breeding plumages in male purple-crowned fairy-wrens and 3D-printed models used in simulated territorial intrusions. Photographs show the three model types used in the model presentation experiments (b, d, f) and the birds they respectively represent (a, c, e): male purple-crowned fairy-wren in nonbreeding plumage (a, b) and breeding plumage (c, d), and northern fantail (control; e, f). Photos: (a) N. Teunissen; (b-e) L. Lermusiaux; (f) M. Fan [Colour figure can be viewed at wileyonlinelibrary.com]

captured to measure tarsus length (a measure of body size). Body size is an important predictor of success in male–male competition generally (Hunt et al., 2009). Tarsus length could be an indicator of male quality in *M. coronatus* as it correlates with song frequency (pitch) in certain male songs (Hall, Kingma & Peters, 2013).

Territory quality was assessed (yearly between 2005 and 2008, and once in 2015) based on the *Pandanus* cover following Kingma et al. (2011a). *Malurus coronatus* generally does not occupy habitat without *Pandanus* (wherein 51% of daytime is spent and 95% of nests are built; Kingma et al., 2011a) and the distribution of *Pandanus* varies considerably within the population.

2.3 | Model presentation experiments

To test whether intruder males in conspicuous plumage are perceived by resident breeder males as a greater threat than males in nonbreeding plumage, we conducted two series of 3D-printed model presentation experiments in 2016. We also tested whether resident breeder males are more aggressive when in breeding plumage themselves and recorded the responses of breeder females to assess their level of interest and aggressiveness. Using 3D-printed models, we avoided any interactive behaviour between live models and residents that could override any potential signal function of coloration (Senar, 2006). Furthermore, because we only manipulated

coloration, we could dissociate its role from the effects of potential confounding factors (e.g., age, body condition or size).

Experiments were conducted in 44 territories (21 with no subordinates, 23 with 1–4 subordinates, mean = 1.4) in May-June (start of dry season, when males were completing the moult out of breeding plumage) and 41 territories (19 with no subordinates, 22 with 1–6 subordinates, mean = 1.2) in October-November (end of dry season, when males were completing the moult into breeding plumage); 38 breeder males and 37 breeder females were tested in both seasons.

Models of male purple-crowned fairy-wrens were printed based on a 3D scan of a taxidermic mount and painted in colours that replicated the natural colours, as assessed by avian visual models (for details see Supporting Information Appendix S1a). We made 19 exemplars of a "brown" male (0% breeding plumage), 19 of a "purple-and-black" male (100% breeding plumage) and two of a northern fantail (*Rhipidura rufiventris*, a bird of similar size; also 3D-printed and painted) used as a control (Figure 2). In each territory, the experiment was replicated with each model type in a randomised sequence, with randomly chosen exemplars. There was a minimum of 3 days between replicates to minimise habituation. For each replicate, we placed the model in a relatively open spot well within the territory (identical for all three replicates when possible) and broadcast a standardised

playback of conspecific contact calls and male solo songs to draw the attention of the territory occupants to the model (see Supporting Information Appendix S1b). One observer (MF) continuously recorded the response of the male and female breeders for a period of 15 min from the start of the playback (see Supporting Information Movie S1). We considered that a focal individual started to respond when it either a) started to sing or b) entered a 3-m radius around the model for the first time, and no longer responded when it a) did not sing and b) was > 3 m from the model, for 3 consecutive minutes. We measured (a) latency of response—time between start of the playback and start of the focal individual's response; (b) duration of response; (c) closest approach; (d) time spent within 3 m of the model; (e) time spent within 1 m; and (f) number of songs (solos and duets); and recorded other aggressive behaviours (swooping, pecking). All presentations in which models were not detected (too distant or not sufficiently visible to be seen by the focal individual; see Supporting Information Appendix S1b) were excluded from further analysis ($n = 38$ of 254). We also recorded the date and time of the day (hourly), substrate type (soil, gravel, stone, rock, wood, grass or leaf litter) and sun strength (from 0 = overcast to 3 = sunny, clear sky). Experiments started at least 30 min after sunrise and ended early afternoon (except for one replicate; see Supporting Information Appendix S1b). No experiment was conducted on rainy and/or windy days.

2.4 | Statistical analyses

We investigated the role of the extent of breeding plumage in male–male interactions by analysing whether it (a) depends on intrinsic and environmental factors (to test for condition-dependence) and (b) predicts the likelihood of subordinates gaining a breeder position. Furthermore, we tested (c) whether breeding plumage of simulated male intruders affects the strength of territorial defence by resident breeder males (and females), and whether this varies with resident male plumage state, using 3D-printed models displaying either extreme of the plumage state range ("purple-and-black" vs. "brown" plumage).

All analyses were carried out in R 3.4.0 (R Core Team, 2017). Linear mixed models (LMM) were built using the packages LME4 (Bates, Maechler, Bolker & Walker, 2015) and LMERTEST (Kuznetsova, Brockhoff & Christensen, 2015). Generalised LMMs (GLMM) were first fitted as generalised linear models without random term to estimate dispersion. If data were under- or overdispersed, appropriate models were selected (see below). All continuous explanatory variables were centred.

2.4.1 | Intrinsic and environmental effects on the extent of breeding plumage

We obtained 279 records of maximum extent of breeding plumage from 108 males over a 6-year period. We built an LMM with the maximum % breeding plumage in a given year as the response variable, and age, within-group rank, tarsus length, territory quality and group size as fixed effects. Bird identity, territory identity and year were included as random intercepts to account for non-independence in the data. Within-group rank was assessed on 01 October, when prebreeding moult is on average completed at the population level (Fan et al., 2017). All breeders were assigned a rank of 1 and subordinates a rank that ranged from 2 to 7 depending on how many other subordinate males were present in the territory and their relative age (the oldest male had a rank of 2, the second oldest a rank of 3, etc.; subordinates of the same age had the same rank). For subordinates, this reflects their rank in the queue for inheriting a breeder position (Kingma et al., 2011b). This analysis was first restricted to birds whose age was accurately known ($n = 129$ banded as nestlings), but as the maximum % breeding plumage only varied significantly between the first and second year (Supporting Information Tables S1 and S2; see Supporting Information Appendix S2a), it was repeated using two age classes, "1" and "2+", with all birds of unknown age but known to be at least 2 years old ($n = 120$) included in the "2+" class. When using age classes, we included the age*within-group rank interaction.

2.4.2 | Competitive acquisition of a breeder position

We tested whether the maximum extent of breeding plumage predicted the likelihood of gaining a breeder position elsewhere among subordinate males at the population level ($n = 53$). We therefore excluded cases of inheritance ($n = 12$) or splitting of the natal territory ($n = 13$), as well as when prebreeding moult was temporarily interrupted for > 6 weeks ($n = 22$; for details see Fan et al., 2017). We used a GLMM with penalised quasi-likelihood (GLMMPQL; underdispersion because many individuals did not obtain a breeder position) using the package "MASS" with the annual status change (became a breeder within the year = 1, did not = 0) as a binomial response variable, and maximum % breeding plumage, age and tarsus length as fixed effects. Due to high correlation between age (levels "1", "2+"; $n = 15$ and 38, respectively) and maximum % breeding plumage ($|r| > 0.7$; Dormann et al., 2013), we fitted these predictors in two separate models. Bird identity nested in territory identity nested in year was included as a random intercept. Although GLMMPQLs may at times yield problematic estimates (see Bolker et al., 2009), the results of the models above appear to be robust as they were quantitatively similar to those obtained when using age in months instead ($n = 45$), as well as when rerunning the models without individuals that died as subordinates before the end of the considered year ($n = 39$)—to account for potential selective disappearance associated with particular extents of breeding plumage (Supporting Information Table S5).

As breeding vacancies primarily arise when a breeder male of a territory dies or, less commonly, moves away, and because subordinate males usually do not disperse far from their natal territory, the opportunity to compete for a vacancy is probably unequal among subordinates, depending on the distance to a vacancy. Therefore, we performed a case-by-case analysis comparing the percentage of breeding plumage of the "winner" of a vacancy at the time it

appeared and other potential competitors at the same time (referred as "losers"). Losers could be either 1) other within-group subordinate males in cases of inheritance or 2) subordinate males located within the same distance to the vacancy in cases of dispersal (n = 7 inheritance and 22 dispersal cases, each case involving one or more losers; see Supporting Information Appendix S2b). We built an LMM with the difference in % breeding plumage (calculated for all pairs of winners and losers, n = 61) as the response variable, the route used to gain dominance (inheritance or dispersal) as a fixed effect, and winner identity as a random intercept (to control for the fact that winners were compared to multiple losers). A similar LMM was built with the difference in age (in months; calculated for all pairs of winners and losers of known age, n = 34) instead as the response variable.

2.4.3 | Model presentation experiments

Focusing on breeder males only, we tested whether their aggressiveness varied with the 3D-printed model type by investigating five variables (four were fitted in LMMs and transformed to ensure normal distribution of residuals): (a) duration of response (*sqrt*-transformed), (b) closest approach (*sqrt*-transformed), (c) time spent within 3 m (*log*-transformed), (d) time spent within 1 m (*log*-transformed) and (e) number of songs—fitted in a negative binomial model using the package GLMMADMB (non-zero-inflated overdispersion). Physical aggression towards the model occurred in only seven instances (see Supporting Information Appendix S2g); this behaviour was therefore not analysed statistically. For all analyses, we fitted 3D model type (levels "control", "brown", "purple-and-black"), territory quality, group size, presence of fledglings in the group (yes/no), season (start/end of dry season), replicate number (1–3), time of the day and sun strength (0–3, which may affect colour perception; Romero, Hernández-Andrés, Nieves & García, 2002) as fixed effects. Latency of response (independent of model type: Kruskal–Wallis test, $\chi_2^2 = 1.69$, p = 0.43) was also included as variation in the duration of playback heard might affect aggressiveness. Age in years was also included; because it was highly correlated with dominance tenure (i.e., time spent as a breeder; |r| = 0.84) and fitting either variable gave similar results (no effect of either), we only reported the results for age. We also included the presence of within-group subordinate males unrelated to the breeder male (yes/no) and to the breeder female (yes/no) as the presence of reproductive competitors (unrelated males) could affect aggressiveness of the breeder male. Model exemplar, date and substrate type were fitted as random intercepts, whereas bird identity was fitted as both a random intercept to allow for individual variation in baseline responsiveness and a random slope, varying with model type to allow for individual variation in the degree of escalation. We compared the full statistical model including 3D model type with the reduced model excluding it to check for the overall effect of 3D model type using a likelihood-ratio test. Post hoc comparisons between 3D model types were performed using Tukey's Honest Significant Difference test. In addition, we carried out a principal component analysis on the five response variables to summarise

variation in aggressiveness (detailed in Supporting Information Appendix S2c), which provided similar results.

We also tested whether the overall response differed between male and female breeders using the data from both sexes and similar statistical models, but fitting 3D model type, latency of response, sex, territory quality, group size, presence of fledglings, season, replicate number, time of the day and sun strength as fixed effects, and bird identity, territory identity, model exemplar, date and type of substrate as random intercepts. As we could not fit a "sex*3D-printed model type" interaction to investigate sex differences in degree of escalation, we then focused on females only and used models similar to those for males (for details see Supporting Information Appendix S2d).

To test whether aggressiveness of breeder males varied with their extent of breeding plumage, we included the percentage of breeding plumage of focal males at the time of the experiments in all the analyses described above. This variable was highly correlated with "season" (|r| = 0.91; 90% of males had ≥90% breeding plumage in October–November, and 86% had <50% in May–June); therefore, we only assessed this effect within each season in separate models, in which % breeding plumage of the focal male was included as a fixed effect and "season" excluded.

3 | RESULTS

3.1 | Intrinsic and environmental effects on the extent of breeding plumage

The maximum extent of breeding plumage produced in a given year was related to age: males produced a more complete breeding plumage as they aged (quadratic relationship between age in months and maximum % breeding plumage achieved; Supporting Information Table S1a). This effect flattened out after 2 years of age, with 1-year-old males developing a less complete breeding plumage (mean = 45%, range: 5%–100%) than males in older age classes, and no significant difference between 2-year-old and older males (respective means (ranges): 93% (35%–100%) vs. 100% (98%–100%); Supporting Information Tables S1b and S2). When using only two age classes, "1" and "2+", the strong effect of age on the maximum percentage of breeding plumage remained (Supporting Information Table S3, Figure 3). Only 16% (4 of 25) of first-year males developed a complete breeding plumage, compared to 92% (206 of 224) of males in their second year or older (all 3-year-old and older males achieved ≥98%).

The maximum extent of breeding plumage was also related to social status as breeder males produced a more complete breeding plumage overall than subordinate males in their group (Supporting Information Table S3, Figure 3). Individual tarsus length, territory quality and group size had no effect on the extent of breeding plumage attained (Supporting Information Table S3).

3.2 | Competitive acquisition of a breeder position

Within social groups, the maximum extent of breeding plumage achieved by subordinate males was related to age relative to other within-group subordinate males (i.e., rank, in the queue for breeder
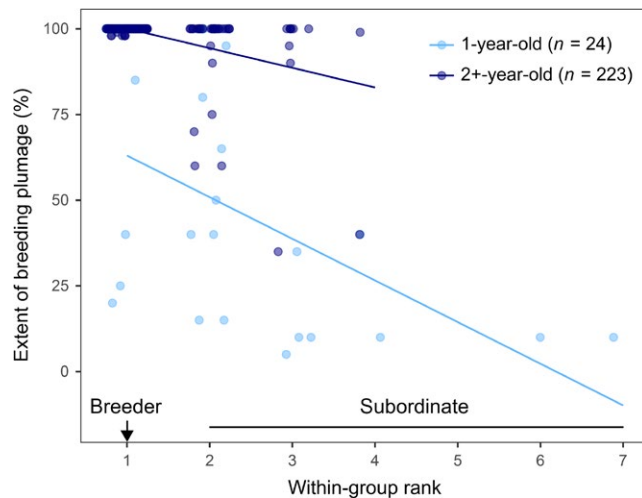
FIGURE 3 Within social groups, breeder males produce a more complete breeding plumage than subordinate males, and among subordinate males, those that are older, and therefore higher-ranked in the social hierarchy, produce a more complete breeding plumage. Moreover, breeding plumage in ≥ 2-year-old males is less affected by within-group rank than in 1-year-old males. Shown is the effect of the interaction of age and within-group rank on % breeding plumage achieved (age: β = 38.77 ± 2.82, t_{225} = 13.73, $p < 0.001$; rank: β = −12.19 ± 1.64, t_{232} = −7.45, $p < 0.001$; age × rank: β = 5.93 ± 1.93, t_{200} = 3.08, $p = 0.002$). Dots depict the (horizontally jittered) raw data, and lines the linear regression lines [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 4 At the population level, subordinate males that produce a more complete breeding plumage increase their chances to gain a breeder position by dispersal within that year. Shown is the effect of maximum % breeding plumage on the likelihood of gaining a breeder position elsewhere. Dots depict the raw data for subordinates that did and did not become a breeder (area indicating the number of observations), the dashed lines the upper and lower limits, and the solid line the predicted correlation (β = 0.11 ± 0.03, t_{14} = 3.07, $p = 0.008$) [Colour figure can be viewed at wileyonlinelibrary.com]

position inheritance): subordinate males that were older produced a more complete breeding plumage than their younger group-mates, an effect that was greatest among comparisons with first-year males (Supporting Information Table S3, Figure 3).

At the population level, the maximum extent of breeding plumage achieved by subordinate males in a given year, but not their age, predicted their probability to gain a breeder position by dispersal in that year: subordinate males producing a more complete breeding plumage increased their chances of becoming a breeder elsewhere (Supporting Information Table S5, Figure 4). Tarsus length did not predict whether males obtained a breeder position (Supporting Information Table S5). Similar results were obtained when excluding individuals that died as subordinates before the end of the considered year (Supporting Information Table S5).

Consistent with this, the case-by-case analysis indicated that the extent of breeding plumage predicted success in obtaining a breeder position: males with more breeding plumage than nearby competitors at the time the vacancy appeared were more likely to fill the vacancy (Supporting Information Table S6, Figure 5a). Age also predicted success: older males were more likely to fill the vacancy than younger males (Supporting Information Table S6, Figure 5b; for further analysis see Supporting Information Appendix S2b).

3.3 | Model presentation experiments

The likelihood that individuals detected the model was high (>80%): 46 breeder males detected the 3D-printed model in 216
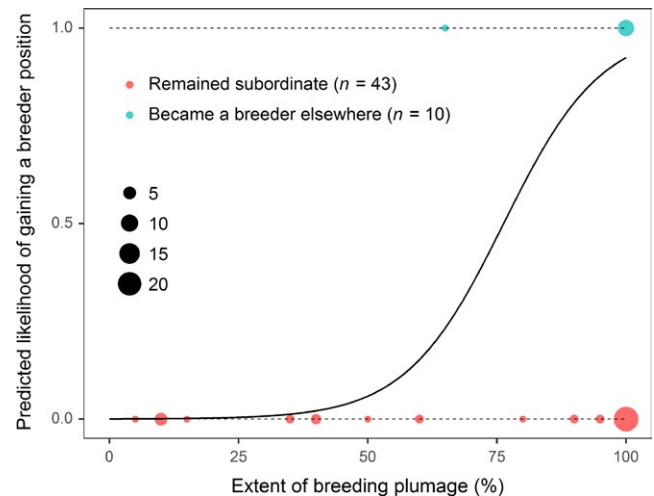
(of 255) experimental replicates (72 control, 74 brown, 70 purple-and-black) and 47 females did so in 210 replicates (69 control, 72 brown, 69 purple-and-black). For males, model type significantly affected the duration of response (likelihood-ratio test, χ_2^2 = 12.98, $p = 0.002$), the closest approach (χ_2^2 = 8.52, $p = 0.01$) and the time spent within 3 m of the model (χ_2^2 = 13.49, $p = 0.001$). Post hoc pairwise comparisons of 3D model types showed that males responded for longer, approached closer and spent more time within 3 m of purple-and-black models, compared to both brown and control models (the difference in closest approach to purple-and-black and brown models was marginally nonsignificant; Supporting Information Table S7c, Figure 6a–c). However, none of these variables differed significantly between the brown and control models (Supporting Information Table S7c, Figure 6a–c). In contrast, 3D model type had no effect on the time spent within 1 m of the model (likelihood-ratio test, χ_2^2 = 3.16, $p = 0.21$) and the number of songs performed (D_2 = 2.43, $p = 0.30$; see also Supporting Information Table S8c, Figure 6d). Females always responded less strongly than males (Supporting Information Table S10) and we found no evidence that their response was affected by the type of model used (likelihood-ratio test, duration: χ_2^2 = 3.84, $p = 0.15$; closest approach: χ_2^2 = 3.54, $p = 0.17$; number of songs: D_2 = 0.71, $p = 0.70$; see also Supporting Information Table S11). There was no indication that male response was affected by the behaviour of other group members (Supporting Information Table S12; see Supporting Information Appendix S2e).

Aggressiveness was also related to territory quality: breeder males occupying lower quality territories were more aggressive as they
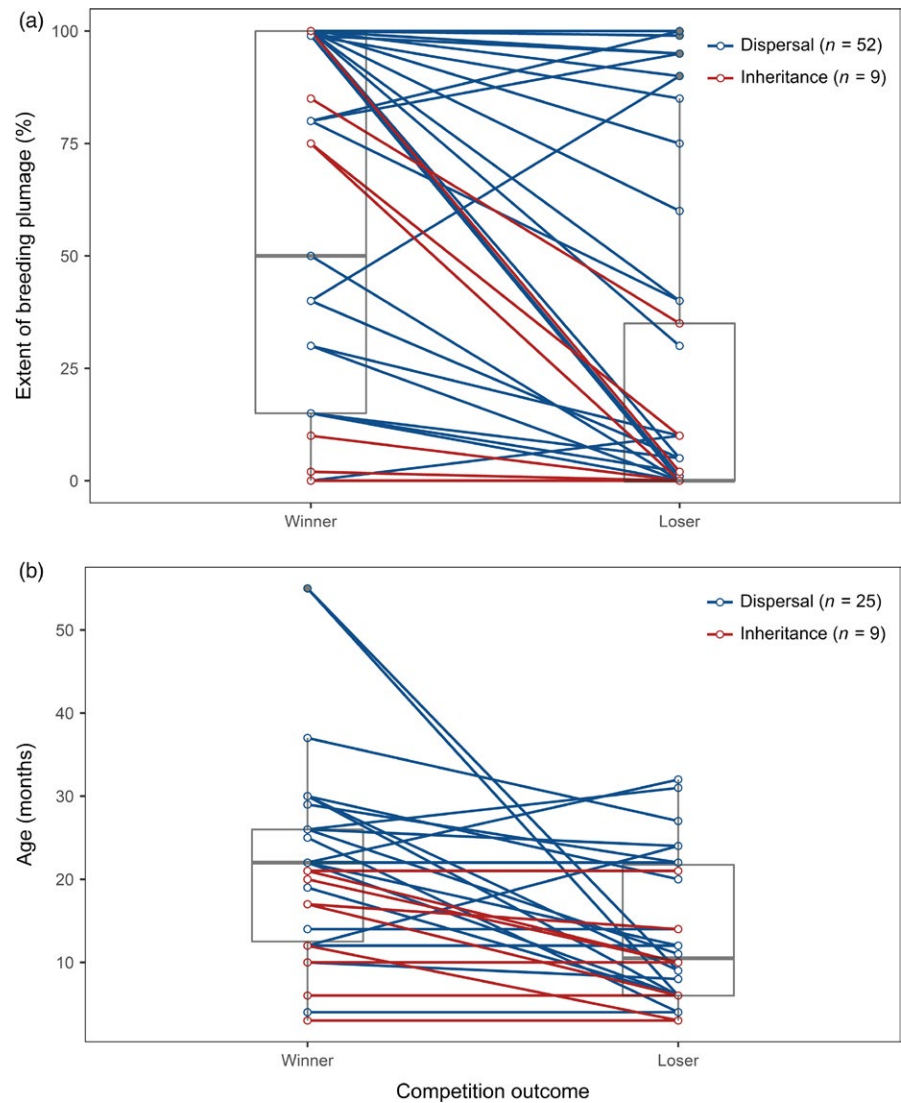
FIGURE 5 Subordinate males that are older and/or display a more complete breeding plumage have higher chances to inherit a breeder vacancy or acquire it elsewhere (when a breeder without a successor dies or moves away). Shown are (a) % breeding plumage and (b) age of winners and losers of competitions for breeder vacancies. Lines depict the pairwise comparisons (difference in % breeding plumage: $\beta = 26.17 \pm 7.66$, $t_{24} = 3.42$, $p = 0.002$; in age: $\beta = 9.43 \pm 2.97$, $t_{22} = 3.18$, $p = 0.004$). Grey boxplots depict the interquartile range (box), medians (dark line) and 2.5% and 97.5% quantiles (whiskers) for winners vs. losers. In inheritance cases, the winner always displayed a similar or larger extent of breeding plumage than the loser, and for brothers of the same age, the one with more breeding plumage inherited the vacancy most of the time [Colour figure can be viewed at wileyonlinelibrary.com]

responded for longer, approached closer, spent more time close and performed more songs (Supporting Information Tables S7a and S8a), independently of the model type (i.e., no significant interaction between the effects of territory quality and 3D model type; Supporting Information Table S13; see Supporting Information Appendix S2f). Moreover, males were significantly more aggressive during the period when they usually moult out of breeding plumage (May–June) than when they usually moult into breeding plumage (October–November; Supporting Information Tables S7a and S8a). However, because the two experimental periods differed in the percentage of breeding plumage of breeder males (most males were mostly brown in May–June and fully purple in October–November), the biological significance of this result must be interpreted with caution. When examining each season separately, we found no indication that the percentage of breeding plumage of breeder males affected their aggressiveness (May–June: $\beta = 0.02 \pm 0.03$, $t_{47} = 0.70$, $p = 0.49$; October–November: $\beta = -0.005 \pm 0.03$, $t_{37} = -0.17$, $p = 0.87$). In all these analyses, age, group size, presence of subordinate males unrelated to either breeder, replicate number and time of the day had no effect on the level of aggression (Supporting Information Tables S7a and S8a).

4 | DISCUSSION

Our findings show that the extent of breeding plumage achieved by males increased both with their age and within-group rank. In addition, it appeared to be a strong predictor of success in male–male contests for the acquisition of a breeding territory, with subordinate males in more complete breeding plumage being more likely to win a breeder position. Simulated male intruders in breeding plumage received more aggression from resident breeder males than those in nonbreeding plumage. Taken together, our results strongly suggest that the conspicuous breeding plumage of male *M. coronatus* functions as an intrasexual signal of dominance and competitiveness.

4.1 | Obtaining a breeder position

In *M. coronatus*, subordinate males very rarely (<1%) reproduce until they gain a breeder position (Kingma et al., 2009). This is achieved by inheriting a position in the natal territory or by dispersing, usually to a neighbouring territory, and may occur at any time of the year depending on the time of disappearance of a breeder (Supporting
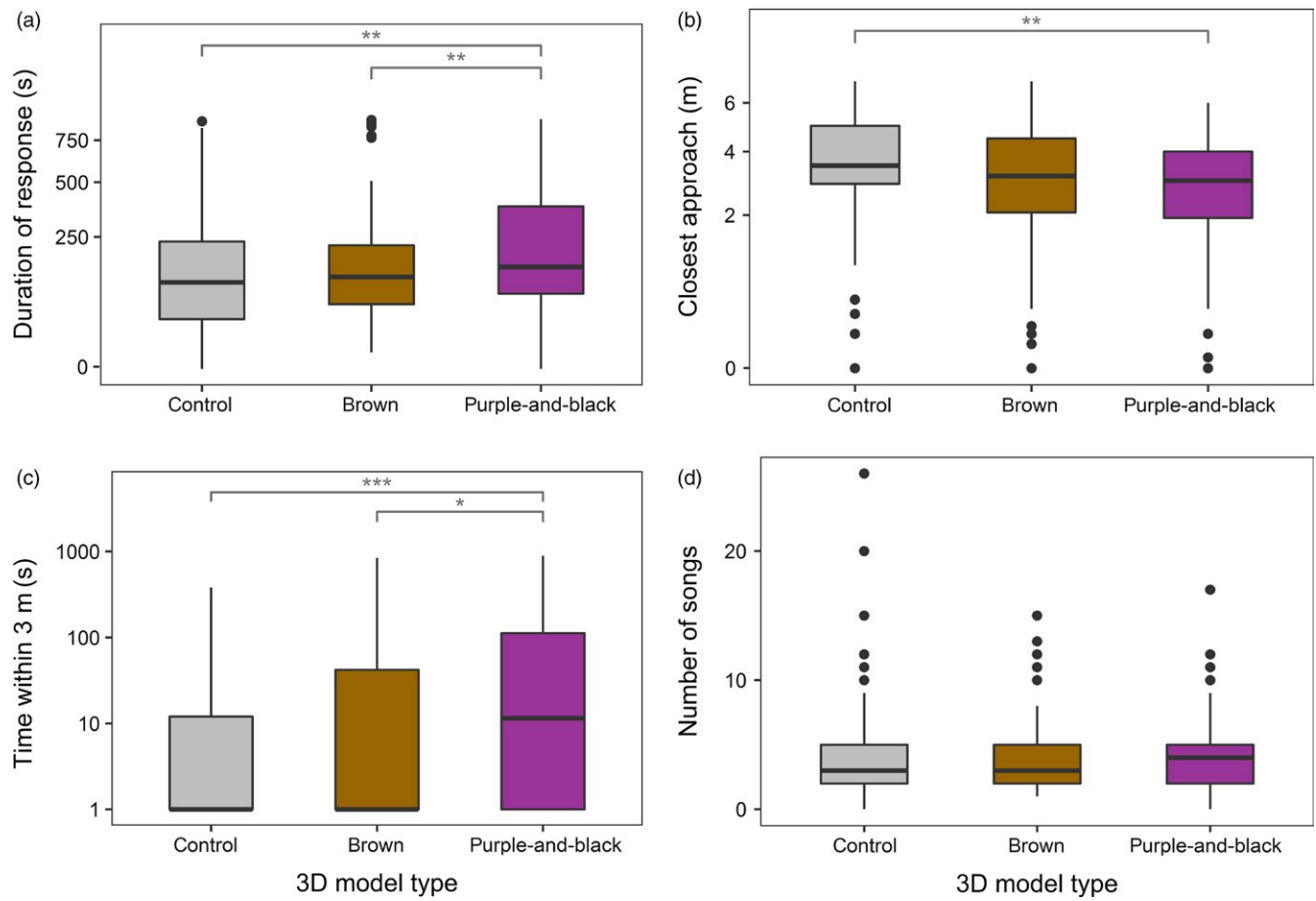
FIGURE 6 Simulated intruders in breeding plumage are perceived as a greater threat to breeder males. Breeder males (a) respond for longer, (b) approach closer and (c) spend more time within 3 m of purple-and-black models compared to brown and control models; however, (d) the number of songs they perform is independent of 3D model type (n = 216). Boxplots depict the interquartile range (box), medians (dark line), 2.5% and 97.5% quantiles (whiskers) and outliers (black dots). Significant pairwise differences are indicated as follows: *p < 0.05, **p < 0.01, ***p < 0.001 (see Supporting Information Tables S7c and S8c for tests statistics). The *y*-axis scale is *sqrt*-transformed in (a, b) and *log*-transformed in (c)

Information Table S4; see Supporting Information Appendix S2b). Inheritance involves no overt aggression between subordinates within groups and appears mostly to occur through an orderly, age-based queue (Kingma et al., 2011b). When ranking each subordinate male by its relative age in the social group, we found that higher-ranked subordinates produce a more complete breeding plumage (Figure 3), and the extent of breeding plumage of subordinate males correlates with their likelihood of inheriting a breeder position. It is possible that higher-ranked (older) males invest more in acquisition of the breeding plumage, and lower-ranked males refrain from doing so as this reflects their relative prospects for social improvement in the near future. Lower-ranked males may thereby also reduce the aggression received from higher-ranked males (Doucet, McDonald, Foster & Clay, 2007; Karubian, Sillett & Webster, 2008), as the results of the simulated territorial intrusions suggest that males in breeding plumage present a greater perceived threat (see below). Alternatively, lower-ranked subordinates may be physiologically suppressed by higher-ranked individuals ("stress of subordination" or "psychological castration"; Reyer, Dittami & Hall, 1986; Creel,

2001; Brouwer et al., 2009), which constrains the development of their breeding plumage. Either way, less complete breeding plumage of subordinate males in groups with higher-ranked males reduces chances for such subordinates to competitively acquire a breeder position elsewhere, indicating an additional unexpected cost for such subordinates.

The extent of breeding plumage predicts the likelihood of gaining a breeder position. At the population level, subordinates with more complete breeding plumage are more likely to competitively take over a vacant breeder position outside of their natal territory that year (Figure 4). In addition, on a case-by-case basis, males with more complete breeding plumage have greater chances to win a vacancy regardless whether this is achieved by inheritance or dispersal (Figure 5a). Because the extent of breeding plumage is highly correlated with age, and age also predicts competitive outcomes (Figure 5b), the former may serve as a visual signal of age among competitors. However, breeding plumage appears a stronger predictor than age at the population level (Supporting Information Table S5), possibly because it may be easier to assess than male age,

especially by unfamiliar individuals. Taken together, our findings indicate that a larger extent of breeding coloration is associated with increased competitive ability to access a breeder position, similar to observations made in several other bird species (reviewed in Senar, 2006 and Santos, Scheck & Nakagawa, 2011).

4.2 | Territoriality: defence of the breeder position

Simulated territorial intrusions using 3D-printed models of males supported a role for breeding plumage in male–male competitive social interactions. Models in breeding colours elicited stronger aggressive responses from resident breeder males, compared to both brown and control models (Figure 6). This suggests that male intruders in complete breeding plumage are perceived as a greater threat to the resident male, as breeder males, and not females, led the defensive response and displayed higher aggressiveness (Supporting Information Table S10). On the other hand, simulated intrusions by pairs (using playback of duets; Hall & Peters, 2008) have been shown to elicit highly coordinated responses from resident breeding pairs, indicative of cooperative territorial defence. To resident breeder males, an unknown single male in breeding plumage presumably represents a risk of territorial usurpation (which might occasionally occur: we observed 23 cases of breeder dispersal, although we do not know if these were voluntary or evictions by the successor). This finding is also consistent with our observation that subordinate males in a territory generally display less complete breeding plumage than the breeder male, which could be an attempt to signal subordination and avoid within-group agonistic interactions. Similar to that, Karubian et al. (2008) reported that in *M. melanocephalus*, dull brown males are socially subordinate to bright males, and bright caged stimulus males receive higher levels of aggression than dull ones.

Independently of intruders' plumage state, and against expectations, we found that males residing in higher-quality, therefore more valuable, territories displayed less aggression (Supporting Information Tables S7a and S8a). Such males generally live in denser areas but we found no evidence for lower aggression in areas with higher population density (Supporting Information Table S14; see Supporting Information Appendix S2h). Alternatively, if defeated males from lower quality territories are of lower quality or in lower condition, they may be less able to competitively acquire another territory and therefore act more desperately and be more risk-prone (Cain & Langmore, 2016; Grafen, 1987; Wolf, Van Doorn, Leimar & Weissing, 2007).

4.3 | From ornament to armament or loss of function?

Our correlational and experimental results suggest that male–male competition is the selective mechanism responsible for the persistence of male conspicuous breeding plumage, as evident from its importance for obtaining and defending a breeder position. Although we cannot completely rule out the possibility that the extent of breeding plumage is used by resident females to assess potential

mates when they attempt to settle as the new breeder, none of our previous and current findings support this. Our model presentation experiment strongly points to a role of the breeding plumage in male–male competition only, with females displaying limited interest in the simulated intruder, and no apparent discrimination of breeding plumage vs. brown models (Supporting Information Tables S10 and S11), and there is no evidence for female choice or reproductive benefits of early acquisition of the breeding plumage (Fan et al., 2017). This is in strong contrast with closely related *Malurus*, where seasonal timing of acquisition of the male ornamental plumage is critical for female EP mate choice, and thereby for male reproductive success, due to very high EPP levels (Figure 1). Because *M. coronatus'* phylogenetic position is nested within this clade (Marki et al., 2017; Figure 1), male breeding plumage in this species could represent a sexual trait formerly selected by female EP mate choice that underwent a shift in function, being subsequently selected by male–male competition. Alternatively, it is possible that breeding plumage elaboration ancestrally had a dual function, being used in both female choice and male–male competition (as may currently be the case in at least one species; Figure 1), whereby the former function was lost as extreme EPP levels and female EP mate choice disappeared (see Kingma et al., 2009). Until more studies investigate the role of *Malurus* breeding plumage in male–male competition (Peters et al., 2013), we cannot confirm which evolutionary scenario—loss or shift of function—is the most likely, but either way our results highlight greater flexibility in function of sexual ornaments than widely appreciated.

Darwin (1859) already appreciated that when a function of a trait is lost, the trait will disappear unless it has multiple functions or switches functions (Lahti et al., 2009). This is also true for sexual ornaments, but not often considered, with studies generally focusing on co-option of an ornament. For example, a substantial number of studies have shown that ornaments used for intrasexual competition in males and females can also be preferred in mate choice (Berglund et al., 1996; Stern & Servedio, 2017). This is generally explained by the armament-ornament hypothesis, which states that traits used in intrasexual competition become co-opted for intersexual mate choice, because their ability to signal individual qualities is also useful for assessment of potential mates (Berglund et al., 1996). Our study shows that the alternative scenarios, traits used in intersexual mate choice switching function to intrasexual competition, or a dual-function trait losing one function, should also be considered. Such scenarios, and our results, imply that intra- and intersexual functions of ornaments can be gained or lost independently and offer possible explanations for the diversity of sexual ornaments and functions. Because these two mechanisms may differ in the selection they impose on sexual traits (Hunt et al., 2009), a shift or loss of function may be characterised by changes in trait expression or selection switching among multiple signalling components. A growing number of studies investigating sexual traits across different populations, at different times, have demonstrated that sexual selection is subject to fluctuations, which may generate very complex evolutionary dynamics (Miller & Svensson, 2014). Our study of the role of male–male competition in a genus renowned for strong selection through

female mate choice further illustrates the complexity of the interplay between the mechanisms of sexual selection and that our view of how sexual selection works may still be incomplete. More generally, it shows that the integrated studies of both mechanisms of sexual selection and all signal components of an ornamental trait in closely related species, with detailed phylogenetic information, can help to uncover new—or rediscover old—evolutionary scenarios and provide further insights into the complex dynamics of sexual selection.

AUTHORS' CONTRIBUTIONS

M.F., A.P. and K.D. conceived the ideas and designed methodology, analysed the data, and led the writing of the manuscript; all authors collected data, contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.t46100m (Fan et al., 2018).

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