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Original Article

Ornamentation is associated with social costs in male red-backed fairywrens (*Malurus melanocephalus*)

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Sexually-selected ornaments typically confer reproductive benefits, but ornamented and unornamented male phenotypes often co-occur in the same population. Reduced social costs are one potential compensatory benefit of unornamented male phenotypes, but few studies have tested this hypothesis in a natural context. Here we present a field-based experiment testing whether ornamented plumage carries social costs in the red-backed fairywren (*Malurus melanocephalus*), a small Australian songbird that exhibits delayed but flexible plumage maturation. Only one-quarter of 1-yr-old male red-backed fairywrens acquire ornamented plumage, but young ornamented males obtain greater reproductive success than males that retain brown, female-like plumage. We experimentally tested whether ornamented plumage is associated with social costs by implanting brown 1-yr-old males with testosterone to induce molt into ornamented plumage, then recorded the resulting social interactions. Testosterone-implanted males developed ornamentation and were chased and attacked more often by conspecific males than were control-implanted males without ornamentation, supporting the hypothesis that molt into ornamented plumage is socially costly. However, despite these apparent costs, some 1-yr-old males naturally acquired ornamented plumage after pairing with a female. Paired 1-yr-olds who naturally acquired ornamented plumage exhibited smaller home ranges than the unpaired, implanted males in their natal groups. Post-hoc simulations suggested that smaller home ranges could result in fewer interactions with neighbors, meaning smaller home ranges may reduce the social costs associated with acquiring ornamentation. We discuss the aspects of manipulating ornamentation with testosterone and suggest that our results add to growing evidence that social costs can enforce the honesty of sexually-selected ornaments.

Keywords: delayed plumage maturation; honest signals; plumage ornamentation; sexual selection; social costs; testosterone.

Introduction

Ornamentation, such as elaborate coloration or song, is often a key determinant of male reproductive success (Andersson 1994), yet in many species it is common for some males to adopt unornamented phenotypes even when they are capable of breeding (Oliveira et al. 2008). For example, many bird species exhibit delayed plumage maturation, a phenomenon characterized by young individuals not acquiring the adult-specific plumage until a certain age (Hawkins et al. 2012). In songbirds, delayed plumage maturation is often characterized by young males not acquiring the ornamented breeding plumage typical of older males and instead displaying female-like or intermediate phenotypes (Rohwer et al. 1980). Although a lack of ornamentation is associated with sneaker reproductive strategies in many taxa (Taborsky 1994; Emlen 1997; Utami et al. 2002), unornamented young male birds rarely exhibit sneaker reproductive behaviors, and typically obtain lower reproductive success than do older, ornamented males (Grant 1990; Morton et al. 1990; Greene et al. 2000; Webster et al. 2008). These findings suggest that young male birds may adopt unornamented female-like phenotypes as a "best of a bad job" strategy due to costs associated with ornamentation that outweigh the reproductive benefits of exhibiting ornamented plumage at a young age. However, our understanding of the "costs" that constrain the development of ornamented plumage remains limited.

Three hypothesized types of costs of ornamentation have been advanced to explain signal variation among individuals, including delayed signal acquisition in young males. The ecological costs hypothesis proposes that unornamented phenotypes benefit from decreased predation pressure because they are more camouflaged to predators (Dunn et al. 2015; Cain et al. 2019). Alternatively, the physiological costs hypothesis suggests that sexual signals are condition-dependent, such that individual differences in genotype, somatic states, epigenetic states, and other physiological processes determine an individual's ability to produce costly ornamentation (Folstad and Karter 1992; Buchanan et al. 2001; Hill 2011). Under this hypothesis, males

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should produce unornamented phenotypes when physiologically or energetically constrained from producing costly ornamented phenotypes (Rohwer and Butcher 1988). Finally, the social costs hypothesis proposes that costs of ornamentation are receiver-dependent; examples include attracting aggression from conspecifics (Webster et al. 2018), or through increased social interactions negatively influencing physiological processes such as oxidative stress (Tibbetts 2014; Vitousek et al. 2014). This hypothesis predicts that older males experience reduced competition for mating opportunities when they prevent young males from obtaining ornamented phenotypes, and young or competitively inferior males benefit from delayed signal acquisition by clearly signaling their subordinate status to reduce aggression from older males (Lyon and Montgomerie 1986).

Of these three hypotheses, the social costs hypothesis may be best suited to explain signal variation in many birds that exhibit delayed plumage maturation (Hawkins et al. 2012). The ecological costs hypothesis has received mixed support when comparing predation rates across colorful and dull phenotypes (eg, Gotmark 1993; Cain et al. 2019). Similarly, physiology is likely to be an important determinant of individual variation in signal quality in many systems, but experimental tests of the physiological costs hypothesis, such as the costs of elevated testosterone, have produced mixed results (Roberts et al. 2004; Foo et al. 2017; Webster et al. 2018; McQueen et al. 2021). In contrast, the social environment plays an important role in signal expression across many taxa, including in birds (Maia et al. 2012; Dey et al. 2014; Welklin et al. 2021), fish (Munday et al. 2006; Maruska and Fernald 2013), insects (Kasumovic et al. 2011), and mammals (Pradhan et al. 2012). Further, social costs have been shown to be important enforcers of signal honesty in many species (Tibbetts and Dale 2004; Chaine et al. 2013; Ligon and McGraw 2016), but most previous studies of signal honesty have focused on badge-of-status type signals and have not examined sexually-selected ornaments or delayed signal acquisition (but see Conover et al. 2000; Bywater and Wilson 2012). Several observational studies and mount presentation experiments have found support for the social costs hypothesis (see Hawkins et al. 2012 for a comprehensive review), but few studies have combined an experimental approach with observations of free-living animals to test whether acquisition of ornamented plumage is socially costly in natural contexts (Rohwer 1977; Rohwer and Rohwer 1978; Stutchbury 1991; Conover et al. 2000; Berggren et al. 2004). To confirm that social costs are sufficient to explain delayed plumage maturation, the hypothesis should be addressed in free-living animals in a natural context, ideally by manipulating their signals and observing the resulting social consequences (Higham 2014).

The red-backed fairywren (*Malurus melanocephalus*) is a model species for studying the causes and consequences of delayed plumage maturation (Karubian 2002). Older males typically alternate between a red-black ornamented plumage during the breeding season and a brown, female-like plumage during the non-breeding season, but approximately three-quarters of 1-yr-old male red-backed fairywrens spend their first breeding season in the brown plumage, and only one quarter of 1-yr-old males acquire the ornamented, red-black breeding plumage typical of older males (Welklin et al. 2021). All 1-yr-old males, including helper males, are capable of siring offspring, but neither helpers nor brown breeders exhibit sneaker reproductive strategies, and accordingly sire few extra-pair offspring (Webster et al. 2008). Paired brown and ornamented males are typically cuckolded at similar rates (but see Dowling and Webster 2017), but ornamented 1-yr-old males sire more extra-pair offspring than brown 1-yr-old males, resulting in ornamented 1-yr-old males obtaining higher reproductive success than brown 1-yr-old males (Webster et al. 2008; Barron et al. 2025). Similarly, since helper males are unpaired, brown breeders obtain higher reproductive success than helper males because they typically sire some within-pair offspring (Webster et al. 2008). Thus, both pairing and ornamentation are associated with reproductive benefits for 1-yr-old males.

Previous research into the costs of ornamented plumage in red-backed fairywrens has not found support for the ecological costs hypothesis and has found only partial support for the physiological costs hypothesis. Comparison of brown and ornamented male phenotypes revealed similar survival rates, suggesting similar predation pressure, in contrast to the expectations of the ecological costs hypothesis (Karubian et al. 2008), although whether ornamented males behaviorally compensate for potential predation costs has not been investigated in this species (McQueen et al. 2017). Observational tests of the physiological costs hypothesis have revealed that males molting into ornamented plumage are in better body condition (Lindsay et al. 2009; Barron et al. 2013; Welklin et al. 2021), and that the timing of ornamented plumage acquisition may be associated with physiological constraints in older, but not younger males due to differences in when they acquire ornamented plumage. Older males acquire ornamented plumage during the dry season (well before the onset of breeding) and inter-annual variation in timing of molt in older males is tightly connected to rainfall, which likely determines food abundance, a key prediction of the physiological costs hypothesis (Welklin et al. 2021). However, 1-yr-old males acquire ornamented plumage just prior to or during the breeding season when their insect prey is abundant, and as a result, acquisition of ornamented plumage by 1-yr-old males is not associated with climatic factors (Welklin et al. 2021), except in cases of extreme environmental conditions such as wildfire (Boersma et al. 2021). Males that naturally molt into ornamented plumage have higher testosterone levels than males in brown plumage (Lindsay et al. 2009), and experimental tests of the physiological costs hypothesis have revealed that brown males respond to testosterone supplementation by initiating molt and producing ornamented plumage, suggesting that plumage ornamentation is testosterone-dependent (Lindsay et al. 2011). However, brown males appear physiologically capable of increasing testosterone levels to the same level as ornamented males (Barron et al. 2015), and brown males elevate testosterone when given the opportunity to pair with a female (Karubian et al. 2011). Therefore, brown males do not appear to be unornamented due to a physiological inability to elevate testosterone.

Instead, whether or not a 1-yr-old male acquires ornamented plumage appears to be influenced by the timing of social cues that likely trigger physiological changes (Welklin et al. 2021), including the elevation of testosterone and its downstream effects (Khalil et al. 2020, 2023). Specifically, 1-yr-old male red-backed fairywrens do not molt into ornamented plumage until after they have dispersed from their natal group and paired with a female. One-yr-old males pair while in brown plumage, but those who pair with a female during the non-breeding season typically molt into ornamented plumage after pairing, whereas 1-yr-old males that pair during breeding or remain as unpaired helpers at their parents' nest, remain in brown plumage (Welklin et al. 2021). These findings suggest that the benefits of ornamented plumage only outweigh the costs of ornamentation once a male has paired with a female. Since ornamented 1-yr-old males sire more offspring than brown 1-yr-old males, the benefits of ornamentation are likely reproductive (Webster et al. 2008), but the

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nature of the costs causing unpaired males to remain in brown plumage are still unclear. During breeding, older males are more aggressive toward ornamented males intruding on their territory than they are toward brown male intruders (Karubian et al. 2008), so it is possible the costs of ornamentation come from increased aggression from conspecifics. Indeed, neighboring social groups often interact with one another during the non-breeding season when the pre-breeding molt occurs (Welklin et al. 2023), possibly resulting in opportunities for older conspecific males to suppress molt and ornamentation in 1-yr-old males.

Here we experimentally test whether ornamented plumage acquisition carries social costs to better understand why most 1-yr-old male red-backed fairywrens exhibit delayed plumage maturation. We implanted unpaired 1-yr-old males with testosterone to induce early molt into ornamented plumage during the non-breeding season (method established in Lindsay et al. 2011). This experimental manipulation allowed us to test a key prediction of the social costs hypothesis: that ornamented 1-yr-old males, relative to brown same-aged males, receive more aggression (eg, chases and attacks) from older males. We test this hypothesis using a social network approach to quantify rates of aggression toward testosterone and control-implanted 1-yr-old males during dyadic associations within foraging flocks of fairywrens. However, elevated testosterone levels have pleiotropic effects on multiple traits with physiological and behavioral consequences (Wingfield et al. 1990; Ketterson et al. 2009; Khalil et al. 2023), in addition to regulating morphological changes such as molt into ornamented plumage (Lindsay et al. 2011). We interpret the results of this experiment in light of the fact that we cannot rule out undetected behavioral changes as an additional potential cause of differences in aggression received.

In addition to observing testosterone-implanted and brown males, we followed a number of paired 1-yr-old males that naturally molted into ornamented plumage in order to understand how paired 1-yr-old males deal with the potential social costs associated with acquiring ornamented plumage. Following naturally-molting males allowed us to test a second prediction of the social costs hypothesis: that acquisition of ornamentation should be associated with social environments that limit interactions with potential aggressors. Males naturally molting into ornamented plumage were paired to a female, and thus in smaller social groups than the implanted unpaired brown males who were still in their natal social groups. Anecdotally, paired 1-yr-old males appeared to inhabit smaller home ranges than unpaired males, so we tested the hypothesis that paired 1-yr-old males have smaller home ranges than unpaired males and that smaller home ranges are associated with fewer interactions with neighboring conspecific males. Combined, these tests help further reveal why unpaired 1-yr-old male red-backed fairywrens exhibit delayed plumage maturation and provide further insight into how social costs affect signal acquisition in species with variable ornamentation.

Methods

Field methods

We studied a population of color-banded red-backed fairywrens near Lake Samsonvale in Queensland, Australia (27° 16′S, 152° 41′E) over two non-breeding seasons (June through August 2017 and 2018). Red-backed fairywrens at this site typically breed from September through January. Seasons are named for the year the breeding season ends in (ie these years correspond to the 2018 and 2019 seasons). Banding during this study was primarily conducted in June but yearly banding efforts in the population began in 2010. Unbanded adults were captured using mist nets and banded with an ABBBS (Australian Bird and Bat Banding Scheme) aluminum band and a unique combination of three plastic color bands, or two plastic color bands and one colored metal band. We collected a small blood sample (20 to 70 uL) from the brachial vein of adults and determined the age (1 or 2+ years) of unbanded individuals using a skull ossification scale for this species (Lindsay et al. 2009).

All procedures involving animals were approved by the Cornell Institutional Animal Care and Use Committee (IACUC 2009-0105), Tulane University IACUC (2019-1715), the James Cook University Animal Ethics Committee (A2100) and performed under a Queensland Government Department of Environment and Heritage Protection Scientific Purposes Permit (WISP15212314).

Experimental evaluation of the social costs of ornamentation

We experimentally tested whether molt into ornamented plumage is socially costly by implanting brown 1-yr-old males in their natal groups with testosterone implants to induce molt into ornamented plumage ($N = 5$ in the 2018 season and $N = 6$ in the 2019 season) or with control implants that contained no testosterone ($N = 5$ in the 2018 season and $N = 3$ in the 2019 season; Khalil et al. 2020; Boersma et al. 2023). Implants are described in Khalil et al. (2020) and Boersma et al. (2023) and were composed of beeswax (73% by weight) and peanut oil (24% by weight). Testosterone implants included 3% crystalline testosterone by weight (0.5 mg dose) and elevated androgen levels for approximately 14 d after implantation, after which androgen levels sharply declined (Boersma et al. 2023). Males were implanted in late June and July by making a small incision in the skin just above the thigh using medical scissors, then inserting the implant subcutaneously using forceps (see Table S1 for exact timing). Vetbond tissue adhesive was used to close the incision (3M, Saint Paul, MN). All implanted 1-yr-old males were unpaired and had not yet dispersed from their natal social groups that typically included their parents, siblings from the same breeding season, and sometimes older siblings from previous breeding seasons (Welklin et al. 2023). All 11 testosterone-implanted males were in separate non-breeding social groups from one another. All 8 control-implanted males were also in separate non-breeding social groups from one another, but some control and testosterone-implanted males were in the same non-breeding social groups.

After implantation, we monitored molt into ornamented plumage by estimating the percentage of red-black plumage to the nearest 5% and monitored each focal male's associations with other individuals through observations of non-breeding foraging flocks for approximately 1.5 to 2 mo (Welklin et al. 2021). This observation period (July–August) ended just before the start of breeding. During observations, we followed foraging flocks for 15 to 60 min and recorded the identities of all individuals associating every 5 min, recorded flock locations every 5 min using Garmin Etrex GPS units, and recorded the occurrence of all aggressive behaviors (chases and physical attacks; see below) throughout the observations, including the identity of the aggressor and receiver when possible. We refer to each of these samples of flocks at the 5-min mark as "sightings'. Individual red-backed fairywrens were considered associating if they were part of the same foraging flock that moved and vocalized in a coordinated manner; most individuals in these flocks remained within 20 m of one another (Welklin et al. 2023). We generated social networks from these observations and determined the composition of non-breeding social groups following Welklin et al. (2023). Briefly, we generated

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dendrograms using the UPGMA method to organize individuals into trees based on network association scores (Sneath and Sokal 1973), then cut the dendrogram at the bifurcation point associated with the highest silhouette distance score (clustering quality score; Rousseeuw 1987) to identify social groups (Welklin et al. 2023). We attempted to follow all social groups equally, but red-backed fairywrens occupy large home ranges during the non-breeding season and spend most of the day foraging quietly, so we did not find every group on every attempt at observation. Our statistical methods account for differences in observation counts among social groups and focal males. We also collected data on the composition and behaviors of foraging flocks opportunistically while conducting other tasks but did not include these opportunistic sightings in our social networks.

To determine whether ornamented plumage was socially costly, we tested whether the likelihood of a subject being chased or attacked was associated with implant type (testosterone or control). A chase occurred when an aggressor displaced a receiver more than twice in quick succession and an attack occurred if the aggressor made physical contact with the receiver. Attacks were violent—the attacking bird often crashed into the receiving bird and took the receiving bird to the ground. Chases that led to attacks were treated as one aggressive event (attack). We obtained our response variable by creating a network edge list that contained all dyadic associations between implanted males and other red-backed fairywrens recorded during our social network observations (sightings collected every 5 min) and opportunistic sightings. For each dyadic association, we coded whether the conspecific directed any aggression toward the 1-yr-old male. This method helped control for differences in social environment between 1-yr-old males, such that the number of aggressive acts a focal male received was relative to the number of associations with potential aggressors that male experienced. Aggression only came from males, never from females, and a Fisher's exact test revealed that this result was not likely due to chance ($P < 0.001$). Therefore, we restricted our analysis to male-male associations only. Although not experimentally quantified, we observed no obvious behavioral differences (ie aggression as described above, singing, or displays) between control-implanted and testosterone-implanted males.

In addition to implanted males, we followed several brown 1-yr-old males with no implants each year that were still in their natal groups ($N = 4$ in the 2018 season, and $N = 13$ in the 2019 season). Some of these males were in the same social groups as males with implants. These males did not differ from control-implanted males in the number of aggressive acts received ($N = 8{,}213$ associations with other males in 1,828 sightings resulting in 6 aggressive events (1 toward a control-implanted male and 5 toward brown males with no implant), generalized linear mixed model with a binomial distribution: $\chi^2_1 = 0.03$, $P = 0.857$), so we combined these groups to compare to males with testosterone implants. We modeled whether 1-yr-old males were targeted with aggression during each association between a 1-yr-old male and another male using a generalized linear mixed model with a binomial distribution and logit link in the R package "glmmTMB" (Brooks et al. 2017). Our model included implant type (control and no implant versus testosterone implant), the potential aggressor's plumage type (ornamented or brown), and whether the potential aggressor and receiver were in the same non-breeding social group as fixed effects. The focal 1-yr-old male's social group identity and his individual identity (nested within his group identity) were included as random effects. We used a likelihood ratio test to test whether day of year influenced aggression received, but found no support for a date effect, so day of year was not included in the final model. We used the same model structure to separately test whether the amount of red-black plumage a testosterone-implanted male had developed was associated with whether or not he received aggression by including the percentage of red-black plumage (0 to 100%) present on the date of each association as a fixed effect instead of male implant type. Additional versions of these models that included sighting identity as a random effect to control for sightings that included multiple 1-yr-old males returned the same results, but the residual fit of these models suggested severe underdispersion (a sign of an overfit model).

In addition to the unpaired males we followed for our experiment, we also observed a number of paired 1-yr-old males that had dispersed out of their natal groups, paired with a female on a new territory or on the female's previous territory (if her mate had died) and were naturally molting into ornamented plumage (ie without testosterone implants; $N = 5$ in the 2018 season, $N = 2$ in the 2019 season). Two of these naturally-ornamented, paired males had an additional 1-yr-old female in their group who dispersed before the breeding season. These naturally-ornamented males were not initially part of our experiment, so were followed less often than the unpaired 1-yr-old males in their natal social groups that were the focus of our experiment. However, each of these naturally-ornamented males exhibited at least 5% red-black plumage before the start of breeding and therefore provided an opportunity to test whether differences in social context (unpaired vs paired) and cause of ornamentation (testosterone-implant vs naturally induced) affected aggression toward 1-yr-old males molting into ornamented plumage. We compared the aggression received by testosterone-implanted males to these naturally-ornamented males using the same model structure as described above.

Statistical analyses were performed in R (version 4.0.4; R Core Team 2021), and we assessed the residual fit of all models using the R package "DHARMa" (Hartig 2021). *P*-values come from Type II Wald chi-square tests unless otherwise stated.

Home range size and social interactions

During our observations of the naturally molting, paired males, we noticed these males appeared to inhabit smaller home ranges than unpaired 1-yr-old males who were still in their natal groups with their siblings and their parents. This observation led to the hypothesis that smaller home ranges, whether an effect of a smaller group size or an active strategy by molting males, may allow naturally-molting males to avoid interacting with conspecific males while molting. We investigated this hypothesis by first testing whether home range sizes differed between males that were in their natal groups and naturally-ornamented, paired males. Home range sizes were calculated using 85% autocorrelated kernel density estimates (aKDE) using the continuous time stochastic process method described in Calabrese et al. (2016), and as previously described in Welklin et al. (2023). We tested whether home range size varied among three 1-yr-old male plumage and implant classes: (1) testosterone-implanted males, (2) control-implanted males and brown males without implants but in their natal groups, and (3) paired, naturally-ornamented males. We used a linear mixed model with aKDE size as the response variable, plumage and implant class, year, and number of GPS waypoints per male as fixed effects, and social group identity as a random effect. The response variable was log-transformed to improve residual fit, and we compared differences in home range sizes between male classes using estimated marginal means with a Tukey correction to control for multiple tests.

Finally, we conducted a post-hoc simulation to investigate whether unpaired males in their natal groups could have

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decreased the potential social costs of acquiring ornamented plumage by reducing their home range size. For this test, we focused on all of the unpaired males still in their natal groups (including control and testosterone-implanted males) and took advantage of the fact that every GPS waypoint we collected was associated with data showing which individuals the male was associating with at that point in space and time. We then asked whether associations with neighboring males could have been reduced if the unpaired males in their natal groups exhibited home range sizes as small as the paired 1-yr-old males. We began by calculating a "simulated reduced home range" for each of the unpaired males by calculating a series of smaller home ranges at coverages ranging from 5 to 85% aKDE by 1% increments. These percentages represent the percent of a male's GPS waypoints that occur within the core area where the male spent most of his time, with smaller percentages corresponding to smaller home ranges. The coverage for each male that most closely matched the median 85% home range size of the naturally-ornamented paired males (0.85 ha) was chosen as his simulated reduced home range. If an unpaired male's 85% home range was smaller than the median home range size of the paired males, we used his 85% home range as his simulated reduced home range.

We then generated a separate social network for each male that included only the associations that occurred within the male's simulated reduced home range and tested how each unpaired male's associations with males in other social groups differed between his full home range and his simulated reduced home range. We conducted this test using a generalized linear mixed model with a Tweedie distribution to improve residual fit (Dunn and Smyth 2005, 2008). Weighted degree (strength) to males in different social groups was included as the response variable, representing the sum of each male's social connections to males in different social groups (Farine and Whitehead 2015). We used the simple ratio index to calculate social networks (see Farine and Whitehead 2015; Welklin et al. 2023). Home range type (full vs reduced) was included as a fixed effect, and social group identity and individual identity were included as random effects. Separately, to help understand our simulations, we tested whether the change in weighted degree to males in different social groups was related to how much home range sizes decreased between the full and reduced home ranges. We built a linear model using difference in weighted degree as the response variable, a quadratic effect of percent change in home range size as a fixed effect, and social group identity was included as a random effect.

The social networks based on the simulated reduced home ranges included fewer social associations than the networks calculated from the full home ranges due to the fewer observations included in the simulated reduced home ranges. It is possible that any reduction in sample size could result in a change in weighted degree values between the full and reduced networks, so we tested whether differences in samples size could explain the observed differences in weighted degree between the two networks using a permutation test. Permutation tests compare an observed metric, in this case the observed difference in weighted degree between the full the simulated reduced network, to a distribution of randomized values to test whether the observed metric falls within or outside of the randomized distribution. We first created a set of randomized simulated reduced home ranges for each male by randomly sampling the same number of waypoints used to create each male's original simulated reduced home range from his full list of waypoints. We then recalculated the weighted degree metric for each of the social networks associated with these randomized reduced home ranges and repeated this process 1,000 times, generating a distribution of 1,000 randomized weighted degree differences between the full network and the 1,000 random networks. We generated a *P*-value by comparing the observed difference in weighted degree between the full network and the original simulated reduced network to the distribution of differences in weighted degree from the networks associated with the randomized reduced home ranges (Farine 2017). If the observed difference in weighted degree fell within the distribution of randomized differences, it would suggest that the change in weighted degree associated with the reduction in home range size was simply a result of the reduction in sample size between the networks. However, if the observed value was outside of the range of randomized values, it would suggest that a smaller home range size is associated with fewer associations with males in other social groups.

Results

Experimental test of the social costs hypothesis

One-yr-old male red-backed fairywrens implanted with testosterone took on average 16.4 d (range 12 to 23 d; Figure S2) to show ornamented feathers that were visible through binoculars. The extent of ornamented plumage acquired was variable among testosterone-implanted males (range 5 to 100% ornamented plumage), but each testosterone-implanted male produced some red-black plumage during our observations (Figure S3). The only exception was a single testosterone-implanted male that disappeared 13 d after implantation, prior to any molt visible through binoculars (see below). However, multiple males did exhibit visible ornamentation within 13 d of implantation (Figure S2), and recaptures of recently-implanted males revealed that brown feathers from the previous molt typically concealed newly growing red-black feathers during the initial stage of molt into ornamented plumage (ie before we could see the growing feathers with binoculars). Therefore, we retained observations of this male in our analyses for the time before he disappeared because it was likely that conspecifics who were in close proximity to him could see evidence of molt. The results of the main analysis are not affected if we remove observations of this male. Control-implanted males and brown 1-yr-old males with no implant remained in brown plumage throughout the non-breeding season. All testosterone-implanted and control-implanted 1-yr-old males, including brown males with no implant, remained unpaired in their natal groups throughout the non-breeding portions of the study. All chases and attacks directed toward unpaired 1-yr-old males (18 out of 21 aggressive events where we identified the aggressor) came from males and not females (Fisher's exact test $P < 0.001$). In total, we recorded 2,539 sightings of red-backed fairywrens flocks that included 1-yr-old males in our experiment.

Our experiment found support for the social costs hypothesis. 1-yr-old males induced to molt into ornamented plumage with testosterone implants received more aggression than did control males who remained in brown plumage: we observed an average of 0.83 ± 0.44 (mean $\pm$ SE) aggressive events directed at testosterone-implanted ornamented males per 100 associations between testosterone-implanted males and other males, and observed an average of 0.16 ± 0.09 (mean $\pm$ SE) aggressive events directed at control-implanted (brown) males and brown males with no implant per 100 associations (Table 1, Fig. 1). However, among testosterone-implanted males, amount of red-black plumage did not predict the likelihood of receiving aggression ($N = 3,324$ associations among testosterone-implanted males and other

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Table 1. Results from a generalized linear mixed model with a binomial distribution and logit link investigating whether implant type, aggressor plumage type, and social group membership influenced the likelihood of a 1-yr-old male being chased or attacked in 11,533 associations between focal 1-yr-old males and other males in 2,539 sightings of red-backed fairywren foraging flocks.

Fixed effects	Beta	SE	χ^2	Df	*P*-value
Intercept	−7.24	0.88	…	…	
Implant type: testosterone (vs. control and no implant)	2.12	0.81	6.86	1	0.009
Plumage of potential aggressor: ornamented (vs. brown)	1.11	0.59	3.50	1	0.061
Social group of the potential aggressor: same as focal male (vs. different social group)	−2.78	0.59	21.91	1	<0.001

Random effects	Variance	Standard Deviation
Focal male's social group ID	1.59	1.26
Focal male identity	0.34	0.58

The dataset includes 36 1-yr-old males in 24 non-breeding social groups and includes 18 observations of aggression toward 1-yr-old males with an identified aggressor. Testosterone-implanted males were chased and attacked 12 times, whereas control-implanted and males with no implant were chased and attacked 6 times. Including day of year as a fixed effect did not improve the model fit (likelihood ratio test: $\chi^2_1 = 1.23$, $P = 0.268$). Including sighting identity as a random effect returns the same level of statistical significance for each of the fixed effects.

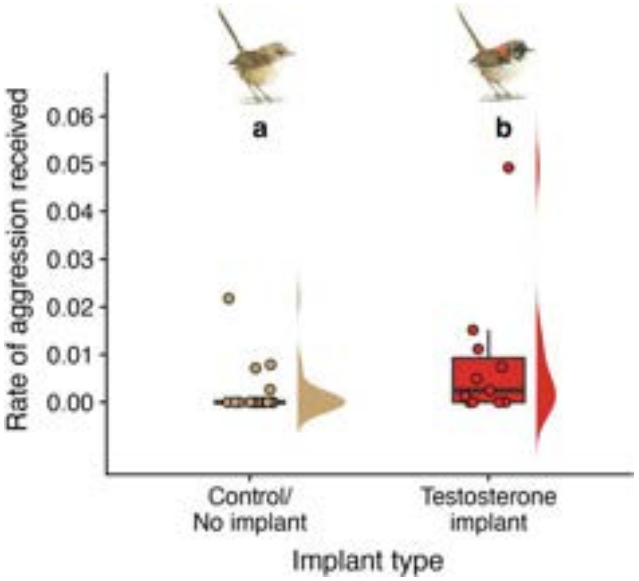

Fig. 1. Rate of aggression (chases and attacks) received in relation to plumage/implant type. Rate of aggression received is calculated for each individual male as the number of associations with other males that involved aggression toward the 1-yr-old male (chase or attack) divided by the total number of associations that male had with other males. All control-implanted males and males with no implant were in brown plumage. Control and no-implant males were equally likely to receive aggression ($N = 8{,}213$ associations, $\chi^2_1 = 0.03$, $P = 0.857$). Aggression toward control/no implant (brown) males differed significantly from testosterone-implanted (ornamented) males (indicated by the different letters (a, b) at the top of the figure). Fairywren drawings courtesy of Allison Johnson.

males in 1,394 sightings resulting in 12 aggressive events with an identified aggressor, $\chi^2_1 = 1.73$, $P = 0.188$, Table S4), suggesting that the presence of ornamentation was associated with receiving aggression, rather than the amount of ornamentation. The three aggressive events for which we did not identify the aggressor, and thus were not included in our models, were directed toward testosterone-implanted males. Aggressive interactions were initiated more often by males from outside the focal male's social group than by a male in the same social group (14 aggressive events by males in different groups, 4 by a male in the same group, Table 1), but aggression was not more likely to come from ornamented males than from brown males (14 aggressive events initiated by ornamented males and 4 aggressive events initiated by brown males; Table 1). Age of the potential aggressor (1-yr-old versus older males) also did not predict the likelihood of initiating an aggressive interaction ($N = 9{,}892$ associations with males of known age in 2,411 sightings resulting in 17 aggressive events with an identified aggressor with a known age, age fixed effect: $\chi^2_1 = 0.88$, $P = 0.348$; Table S5). We observed only one chase of a naturally-ornamented 1-yr-old male by an older ornamented neighbor. After accounting for differences in observation rates, naturally-ornamented males received similar amounts of aggression as testosterone-implanted males ($N = 3{,}509$ associations between 1-yr-old males and other males in 471 sightings of naturally-ornamented males and 1,551 sightings of testosterone-implanted males resulting in 13 aggressive events with an identified aggressor (1 toward a naturally-ornamented male and 12 toward testosterone-implanted males), $\chi^2_1 = 0.83$, $P = 0.363$; Table S6). Day of year did not influence the likelihood of a 1-yr-old male receiving aggression (Table 1).

Chases ($N = 17$) occurred when 1-yr-old males flew away from their pursuer, whereas attacks ($N = 4$) occurred when focal males did not see the potential aggressor, resulting in the aggressor flying quickly and quietly toward the 1-yr-old male from 3 to 10 m away and initiating physical contact (ie, slamming into him and often taking him to the ground). While on the ground, 1-yr-old males produced distress calls and appeared to struggle to escape, but our line of sight was often limited by the tall grass this species frequents. Aggressive interactions toward 1-yr-old males occurred both within and outside of the home ranges of the 1-yr-old males (12 within, 3 outside for aggressive events where location was recorded). We observed no obvious differences in aggressive behavior (initiation of chases and attacks) by 1-yr-old male implant classes: six 1-yr-old males with control implants or no implant initiated aggression 13 times, and we observed two instances of testosterone-implanted males initiating aggression. One testosterone-implanted male chased a female and the receiver in the other aggressive event had brown plumage but was unidentified. Control and testosterone-implanted males were equally likely to pair with a female during the breeding season ($N = 36$, $\chi^2_1 = 0.59$, $P = 0.441$; Table S7).

One testosterone-implanted male disappeared prior to showing signs of molt after being chased by an un-implanted, 1-yr-old brother approximately 13 d after implantation, around the time the implanted male likely would have begun producing ornamented plumage (Figure S2). The chase occurred when the brothers' social group encountered a neighboring social group and the ornamented male from each group began displaying and chasing the female from the neighboring group. The un-implanted brother displaced the testosterone-implanted male from his perch and pursued him far away from the interacting social groups. The testosterone-implanted male finally escaped his pursuer by flying deep into the forest and hiding in a dense bush where he foraged on his own for approximately 20 min, then rejoined his social group. However, the testosterone-implanted male was absent from his social group the next day and was never resighted again, suggesting that he had dispersed off of the field site or died.

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Home range size and social interactions

One-yr-old males implanted with control and testosterone implants exhibited similar home range sizes, suggesting that testosterone treatment did not significantly influence home range size (control vs. testosterone-implanted males: Beta = −0.25 ± 0.13 SE, $P = 0.154$, Fig. 2; Table S8). Instead, unpaired 1-yr-old males in their natal groups in both testosterone and control categories exhibited larger home ranges than paired, naturally-ornamented 1-yr-old males who had dispersed from their natal groups ($N = 41$, control and no-implant males versus naturally-ornamented males: Beta = 1.25 ± 0.38 SE, $P = 0.007$; testosterone-implanted males versus naturally-ornamented males: Beta = 1.5 ± 0.41 SE, $P = 0.002$, Fig. 2; Table S8). The number of GPS waypoints collected for each male did not influence home range size ($\chi^2_1 = 1.69$, $P = 0.194$).

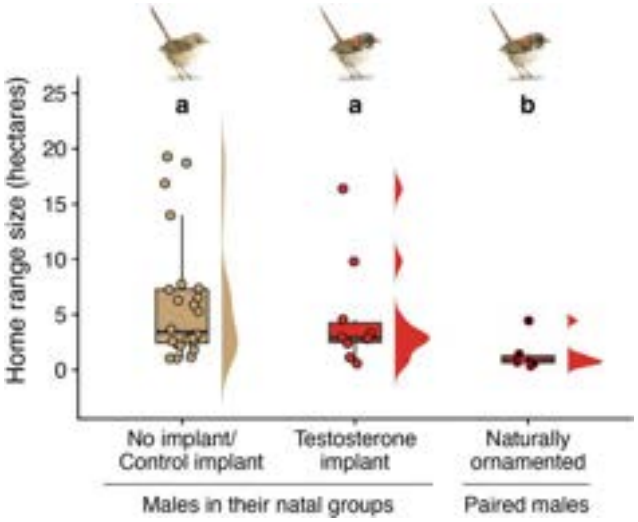

Fig. 2. Home range size of 1-yr-old males by implant type, plumage phenotype, and social status (unpaired males in their natal group vs males paired with a female in their own group) calculated from auto-correlated kernel density estimates (aKDE). Brown males with no implant, males with control implants, and males with testosterone implants were unpaired and in their natal groups. Naturally-ornamented males were paired with a female in a new, non-natal group. Letters above (a, b) show statistically significant differences among categories. Fairywren drawings courtesy of Allison Johnson.

Post hoc simulations suggested that if males in their natal groups had reduced their home range size to that exhibited by the paired, naturally-ornamented males, they could have significantly reduced their rate of associations with males in neighboring social groups ($N = 34$, $\chi^2_1 = 57.55$, $P < 0.001$; Fig. 3, Table S9). Intuitively, the amount each unpaired male's associations to neighboring males decreased in the simulations was associated with how much his home range size was reduced to match the median home range size of the paired, naturally-ornamented males: a negative quadratic relationship revealed that large reductions in home range size resulted in fewer interactions with neighboring males ($N = 34$, $F_{2,25} = 5.21$, $P < 0.013$, Table S10, Figure S11). However, the relationship between the reduced home ranges and fewer interactions with neighboring males was not a consequence of the reduction in sample size required to produce each male's simulated reduced home range. Permutation tests revealed that the observed differences in weighted degree between the full and simulated home ranges were always greater than the differences in weighted degree between the males' full home ranges and the weighted degree metrics associated with the randomized reduced home ranges ($P < 0.001$, Figure S12).

Discussion

Ornamentation often confers reproductive benefits, but young males of many avian species delay acquisition of ornamented plumage until after their first year, despite being capable of breeding (Hawkins et al. 2012). This delay suggests that the costs associated with ornamentation can at times outweigh the

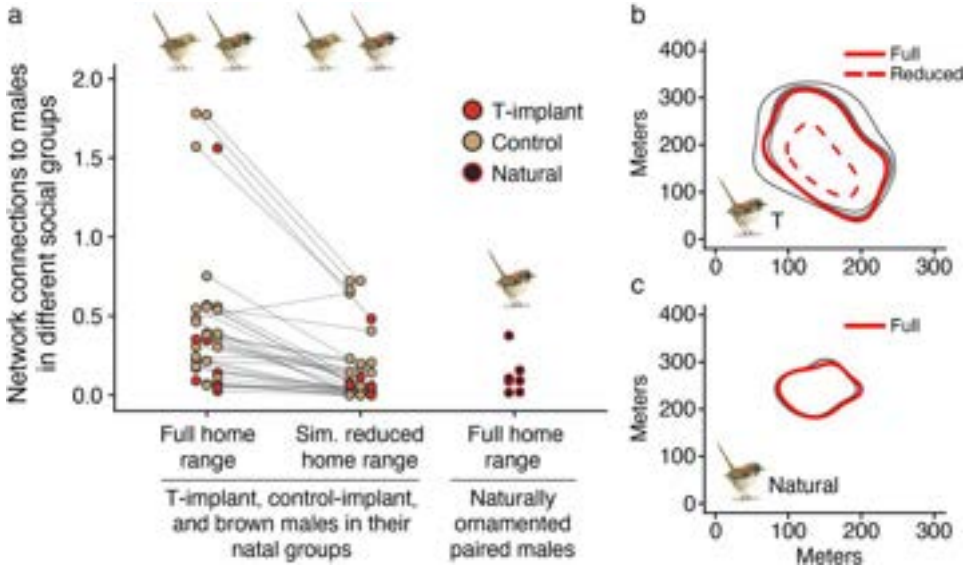

Fig. 3. Home range size and social associations simulation results. a) Social network connections (weighted degree) to males in different social groups for 1-yr-old males in their full home range versus their simulated reduced home range ($N = 34$, $\chi^2_1 = 57.55$, $P < 0.001$). Lines connect individual males. The same metric is also shown for paired, naturally ornamented 1-yr-old males in their full home-range. b) Full (not simulated) geographic home range of one testosterone-implanted male (solid red line), his simulated reduced home range (dashed red line), and the full home ranges of his social group members (gray lines). c) Full (not simulated) geographic home ranges of one naturally-ornamented paired male (red line) and his paired female (gray line). The male's home range was shifted slightly to the right to reduce overlap with his paired female's home range. Full home ranges are plotted from real data (85% auto-correlated kernel density estimates). Fairywren drawings courtesy of Allison Johnson.

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reproductive benefits obtained by young males exhibiting ornamented plumage (Grant 1990; Morton et al. 1990; Greene et al. 2000; Webster et al. 2008). The social costs hypothesis is a leading candidate for functional explanations of delayed plumage maturation in birds (Hawkins et al. 2012) and may be important to maintaining honest signaling more generally (Webster et al. 2018), but few studies have conducted experimental tests of this hypothesis by manipulating the ornamentation of free-living individuals (Rohwer 1977; Rohwer and Rohwer 1978; Stutchbury 1991; Conover et al. 2000; Berggren et al. 2004).

Social costs of ornamented plumage acquisition

Our results show that unpaired, testosterone-implanted male red-backed fairywrens molting into ornamented plumage experienced more chases and attacks than did unpaired, unornamented brown males with control-implants or with no implant. Paired, naturally-molting ornamented 1-yr-old males received similar amounts of aggression as unpaired testosterone-implanted males, suggesting that ornamented plumage, rather than a male's pairing status, was the cause of aggression toward 1-yr-old males molting into ornamented plumage. Amount of ornamented plumage did not predict whether a (testosterone-implanted) male was attacked or not, suggesting that the presence of ornamentation elicited aggression rather than the degree of ornamentation. This result may be explained by the absence of "intermediate-plumaged" males during breeding in this system. During breeding, nearly all males are completely brown, or completely red-black, with very few males exhibiting intermediate stages of ornamentation composed of both red-black and brown feathers (Webster et al. 2008). Therefore, most males that naturally begin molt into ornamented plumage (ie in the absence of testosterone implants, but with elevated endogenous testosterone (Lindsay et al. 2009)) will eventually acquire ornamented plumage within a few weeks (Welklin et al. 2021). This suggests that any 1-yr-old male molting into ornamented plumage may represent a potential reproductive threat to neighboring males because ornamented males sire more extra-pair offspring than do brown males (Webster et al. 2008).

Aggression toward 1-yr-old males was relatively rare in the thousands of social associations we recorded within and among social groups. Yet, due to the violent nature of the agonistic interactions that ended in physical attacks, even one aggressive event could be costly for the receiver. Indeed, one testosterone-implanted male disappeared from the study site within a day of being chased by a brother, suggesting that this male was either forced to disperse or died, emphasizing the potential costly nature of these aggressive interactions. No other 1-yr-old males dispersed from our field site during the study.

Aggression toward ornamented 1-yr-old males came from both young and old males, not only from older males as usually predicted by the social costs hypothesis (Lyon and Montgomerie 1986). This finding may suggest that ornamented 1-yr-old males may pose a threat to both young and old male neighbors. Older males, most of whom are already paired with a female, are likely threatened by the increased competition for reproductive opportunities presented by ornamented 1-yr-old males. In contrast, young males, who often are not paired with a female, may be threatened by the increased competition to pair with a female presented by unpaired ornamented 1-yr-old males, as female red-backed fairywrens are more attracted to ornamented than to brown males (Karubian 2002; Barron et al. 2025). Most aggression toward 1-yr-old males molting into ornamented plumage came from males outside their social group, in contrast to some other species, such as Mute Swans (*Cygnus olor*), in which social costs come primarily from the fathers of young males who chase ornamented offspring from the social group (Conover et al. 2000). Combined, our findings provide support for the social costs hypothesis and indicate that social costs from neighboring males likely maintain the honesty of ornamented plumage in the red-backed fairywren by preventing 1-yr-old males from acquiring ornamented plumage until after they have paired with a female, at which point the costs and benefits of ornamented plumage may change (Webster et al. 2018; Welklin et al. 2021).

There is an important aspect of our study design that needs attention: we used testosterone implants to induce molt into ornamented plumage in 1-yr-old males in this and a previous study (Lindsay et al. 2011). Our previous work has shown that males molting into the ornamented phenotype have higher testosterone titers than those that molt into brown, unornamented plumage (Lindsay et al. 2009), suggesting that testosterone titers are the natural mediator of plumage type. However, testosterone, acting as a phenotypic integrator, also regulates other physiological and morphological processes, including behavior (Wingfield and Hahn 1994; Goymann et al. 2007; Ketterson et al. 2009; Maruska et al. 2013). For example, testosterone supplementation has been reported to influence home range size (Chandler et al. 1994) and increase singing rates (Strand et al. 2008). Our experiment was not designed to separate the potential behavioral effects of testosterone from the effects of ornamented plumage, so we cannot rule out the possibility that testosterone-regulated traits other than molt into ornamented plumage may have elicited aggression from conspecifics. Our implants elevated testosterone for approximately 2 wks (Boersma et al. 2023), but we observed no obvious behavioral differences between testosterone and control-implanted males. For example, there was little or no singing and no displaying by any of the implanted 1-yr-old males in this experiment and ornamented testosterone-implanted males were foraging, not singing or displaying when they were chased and attacked. We also observed very little aggression initiated by testosterone-implanted males, and testosterone-implanted males did not have larger home ranges than did control males (Fig. 2; Table S8), but testosterone-implanted males were still in their natal groups. Therefore, the visual cues of ornamentation are likely the simplest explanation for why testosterone-implanted males received more aggression than brown males, but we cannot rule out the possibility that undetected behavioral differences also contributed to testosterone-implanted males receiving aggression.

Future studies could separate the effects of morphological and behavioral change by manipulating plumage signals with art markers or dye (eg Rohwer 1977) and further test the hypothesis of testosterone pleiotropy as phenotypic integration (Khalil et al. 2023).

Home range size and social interactions

The social costs hypothesis also predicts that acquisition of ornamentation should be associated with social environments that limit interactions with potential aggressors. We found that, compared to testosterone-implanted and control-implanted males that remained in their natal social groups, paired 1-yr-old males ranged over smaller areas during and after molt into ornamented plumage. We do not know whether a small home range size is an active strategy by paired 1-yr-old males molting into ornamented plumage that allows them to avoid interacting with neighbors, or whether it is simply a constraint of establishing a territory in a crowded social environment. If smaller groups require smaller home ranges than larger groups, then group size could offer a simple explanation for why unpaired 1-yr-old males in their natal

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groups exhibited larger home ranges than paired 1-yr-old males, who in most cases were in a group with only their paired female. Our post hoc simulations suggest that unpaired 1-yr-old males could have reduced their associations with males in neighboring social groups if they had reduced their movements to smaller home ranges, such as those exhibited by the paired, naturally-ornamented males, possibly reducing the social costs associated with acquiring ornamentation. However, our observations clearly show that despite the possible benefits of a smaller home range, most of the testosterone-implanted males did not adopt this strategy and exhibited similar home range sizes as control males and exhibited larger home ranges than the paired, naturally-ornamented 1-yr-old males.

Why testosterone-implanted ornamented males did not exhibit small home ranges while molting into ornamented plumage may be explained by social constraints associated with remaining in their natal groups. Red-backed fairywrens are extremely social and rarely forage independently from their social group (Rowley and Russell 1997; Welklin et al. 2023). If paired 1-yr-old males are socially dominant to their female social partner, they may be able to set the pair's territory size, whereas unpaired testosterone-implanted males may have been constrained to following the dominant individuals in their social group, such as their parents who likely benefit from interacting with neighboring social groups. For example, older, ornamented male fairywrens often display to potential extra-pair females in neighboring groups (Mulder 1997; Dowling and Webster 2017), and older females may seek out interactions with neighboring males to assess future extra-pair mates (Varian-Ramos and Webster 2012; Brouwer et al. 2017). Alternatively, unpaired 1-yr-old males themselves may benefit from interacting with neighboring groups to search for unpaired females. Waiting to molt into ornamented plumage until after pairing may be a "best of a bad job" strategy that allows 1-yr-old males to draw less attention from other males until they can pair with a female and settle on a new, smaller territory.

Conclusions

Combined, our experimental and observational results contribute to a growing literature showing that social costs can play important roles in maintaining the honesty of sexual signals (Webster et al. 2018). Such social costs may be particularly important to explaining delayed signal acquisition (Conover et al. 2000; Hawkins et al 2012), especially among young males (Lyon and Montgomerie 1986). Our results indicate that social costs may play an important role in preventing 1-yr-old male red-backed fairywrens from acquiring ornamented plumage until after they have left their natal social group and paired with a female. Once a 1-yr-old male pairs with a female, the reproductive benefits of pairing appear to outweigh the social costs associated with ornamentation (Webster et al. 2008; Welklin et al. 2021). Moreover, our results suggest that acquisition of signals that carry social costs may be associated with social situations that counter those costs, such as smaller home ranges that could reduce interactions with conspecifics. Future studies should consider the possibility that access to both increased benefits and reduced costs associated with a new social situation contribute to variation in sexual signal acquisition in nature.

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Author contributions

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Supplementary material

Supplementary material is available at *Behavioral Ecology* online.

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Conflict of interest

None declared.

Data availability

Analyses reported in this article can be reproduced using the data provided by Welklin et al. (2025).

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