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Reproductive effort of both male and female Bar-throated Apalis *Apalis thoracica* is predicted by ornamentation of self and mate

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Melanin-based plumage ornaments have been shown to play an important role in male–male competition, but also influence inter-sexual communication. Consequently, ornaments may be associated with reproductive effort of both males and females. Females mated to males with larger melanin ornaments may acquire access to better territories or benefit from increased paternal care. Here we investigated whether the melanin-based breast-band of male and female Bar-throated Apalis *Apalis thoracica* is a signal of information about its bearer and is associated with male and female reproductive effort. Breast-band size was a highly variable morphometric trait in both sexes, but only in males was it associated with body mass. We then assessed whether male and female breast-band size predicted maternal and paternal investment. Egg mass increased with male breast-band size, but decreased with female breast-band size. Whether females adjust maternal hormone allocation in response to their partner's ornamentation remains a contentious issue. We found that yolk testosterone and androstenedione concentrations were not predicted by male ornamentation or body mass. Finally, males with larger breast-bands provided their mates with more food, allowing those females to spend more time incubating. Reproductive effort of both parents is therefore predicted by their own and their mate's ornamentation in Bar-throated Apalis, and thus breast-band size potentially acts as a signal of reproductive performance in both sexes. These results highlight the need for more comprehensive analyses of a relationship between melanin-based ornaments and fitness, incorporating multiple behavioural variables associated with reproductive effort.

Keywords: maternal investment, ornamentation, paternal care, sexual selection, yolk hormones.

Secondary sexual traits such as weaponry, song, nuptial plumage or other ornamentation often signal information about the bearer of these traits to conspecifics. Such traits may be used as 'badges of status' indicating fighting ability in contest competition (Rohwer 1975, Clutton-Brock *et al.* 1980,

Senar 2006, Chaine *et al.* 2013), advertise genetic quality (Hamilton & Zuk 1982, Tschirren *et al.* 2012, Johnston *et al.* 2013) or reveal information about the state or condition of the individual, such as hormone levels or parasite loads (Weatherhead *et al.* 1993, Martínez-Padilla *et al.* 2014), or about the mating strategy adopted by the bearer (Wingfield *et al.* 1990, van Dijk *et al.* 2012). They may also signal direct benefits to mates in terms of

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access to a high-quality territory, increased mate feeding rates during incubation, and increased parental investment in rearing offspring (Hoelzer 1989, Voltura *et al.* 2002, Hill & McGraw 2006). Secondary sexual traits thus play a central role in the life-history of many animals.

In birds, colour variation in sexually selected plumage ornaments is usually due to carotenoid and melanin pigmentation or to structural coloration (Hill & McGraw 2006). Specifically, melanin-based plumage coloration has been shown to function in male–male competition and in social competition outside the breeding season (Jawor & Breitwisch 2003, Tibbetts & Safran 2009, Chaine *et al.* 2013), but also to play an important role in inter-sexual communication, conveying information about morphology, physiology and behaviour, including territory defence and parental investment (Jawor & Breitwisch 2003, van Dijk *et al.* 2012, Da Silva *et al.* 2013). Melanin-based ornamentation may thus serve simultaneously as an intra- and inter-sexual signal and can consequently be expected to influence the optimal allocation of resources of a breeding pair among multiple costly life history traits and be an important predictor of individual fitness of both male and female parents (Anderholm *et al.* 2004, Bókony & Liker 2005, Freeman-Gallant *et al.* 2010, van Dijk *et al.* 2012).

Although previous research has made important progress in understanding the mechanisms, evolutionary drivers and fitness consequences of melanin-based ornamentation in a variety of contexts (Jawor & Breitwisch 2003, Bókony & Liker 2005, Freeman-Gallant *et al.* 2010, Lattin & Romero 2013), the question of how ornamentation is involved in shaping social interactions remains of major interest (Houston *et al.* 2005, Tobias *et al.* 2012, Chaine *et al.* 2013). One example of such social interaction is that between parents, for which mate choice, territory defence and parental investment may all be influenced by ornamentation of the male and female (Houston *et al.* 2005, Clutton-Brock 2009). Differential allocation of parental investment in rearing of offspring in response to the partner's ornamentation is known to play an important role (Burley 1986, Hoelzer 1989, Sheldon 2000). One way in which a female parent may adjust investment in reproduction in response to her partner's ornamentation is through maternal effects (Mousseau & Fox 1998). A maternal effect that has attracted much attention is the differential transfer of maternal hormones to the

offspring via the eggs (Schwabl 1993, Groothuis & Schwabl 2008). Yolk levels of testosterone (T) and its precursor androstenedione (A4) can vary adaptively within and between clutches (Gil 2003, Groothuis *et al.* 2005), may be influenced by the social environment (Hargitai *et al.* 2009, Safran *et al.* 2010, Remeš 2011, van Dijk *et al.* 2013), and can significantly affect growth and survival of individual offspring (Sockman & Schwabl 2000, Eising *et al.* 2001, Hadfield *et al.* 2013), with long-lasting effects on morphology and behaviour (Schwabl 1993, Strasser & Schwabl 2004, Eising *et al.* 2006, von Engelhardt & Groothuis 2011). In particular, melanization may reflect levels of circulating T and thus an individual's competitiveness or levels of social stress (McGraw *et al.* 2003, Laucht *et al.* 2010), which in turn may influence maternal deposition of yolk T. This highlights the link between hormone transfer, melanization and behaviour (Bókony *et al.* 2008). Therefore, melanin-based female ornamentation may be associated with maternal allocation of yolk androgens. Additionally, studies of how females adjust maternal hormone allocation, and more generally reproductive investment, in response to their mate's ornamentation have produced conflicting results and this topic remains a contentious issue (Kindsvater & Alonzo 2014). In some studies, yolk hormone concentrations were higher when females were paired with males of higher perceived quality (Gil *et al.* 1999, Tanvez *et al.* 2004, Loyeau *et al.* 2007, Remeš 2011), but in others no effects or negative effects were found (Rutstein *et al.* 2004, Marshall *et al.* 2005, Horváthová *et al.* 2012, Parisier *et al.* 2012). These mixed outcomes suggest that multiple ecological factors may affect the functional relationship between plumage signals of quality and a multitude of reproductive traits. It is striking therefore that many studies investigating female response (e.g. clutch-size or deposition of maternal yolk hormones) to male ornamentation have largely ignored behaviour associated with mate quality, such as courtship feeding or male parental care (but see Laaksonen *et al.* 2011). A recent study showing how males specifically affect female and offspring fitness is key to understanding the occurrence and direction of differential allocation (Kindsvater & Alonzo 2014).

Here we assess whether the size of a melanin-based plumage ornament, the black breast-band, in males and females of the south-temperate, socially monogamous Bar-throated Apalis *Apalis thoracica*

is associated with male and female body mass and size, and whether it predicts multiple components of reproductive effort. In Bar-throated Apalis, incubation is carried out solely by females, which are provisioned at the nest by their mates. We first test the hypothesis that the melanin-based breast-band is a predictor of male and female quality and predict that breast-band size of males and females is more variable than non-sexually selected traits. Secondly, we assess whether male reproductive investment is predicted by male breast-band size and whether males with wider breast-bands provide more food to their females. Finally, we assess whether females adjust maternal investment in response to their own and their mate's breast-band size, and whether female incubation is predicted by male breast-band size.

METHODS

Study area and species

Bar-throated Apalis were studied at Koeberg Nature Reserve, Western Cape Province, South Africa (33°41'S, 18°27'E), an area of coastal dwarf scrubland. Between August and October 2005, 25 Apalis territories were monitored from nest building through to chick rearing. We caught 23 males and 19 females on 23 different territories using mist-nets and call playbacks. Birds were fitted with a numbered aluminium ring and three colour rings for individual recognition. Tarsus length was measured with a Perel digital calliper, wing length with a wing ruler and body mass with a portable digital balance (TFT-100). Phenotypic measurements were not related to capture date (all $P > 0.180$). Females were caught on average 7.42 ± 1.69 days prior to the nearest egg-laying event and time to egg-laying did not significantly affect female body mass ($P = 0.12$). However, one female was caught on the same day as she laid an egg and therefore her body mass was corrected for the mass of the egg she laid.

Three digital photographs per individual were taken at a fixed distance of approximately 20 cm with an Olympus C350Z digital camera in daylight conditions, using a fixed focal length of 17.4 mm. The bird was held facing the camera alongside a ruler. Each bird was repositioned before taking a repeat photograph. All birds were held and photographed by the same person (C.M.E.). Breast-band sizes of both sexes (22

males and 18 females) were determined from these digital photographs through analysis in Corel PHOTO-PAINT 12 (Corel Corp., Ottawa, Canada). Contours of breast-bands and the adjacent ruler were traced and the number of pixels within the contours was determined, after which pixel number was transformed to surface area in mm^2 . Repeatability (*sensu* Lessells & Boag 1987) of breast-band size measurements between multiple photographs of the same bird was 80%. The averages of three breast-band size measurements per individual were used in the analyses. For one male and one female only one high-quality image was available and these were used in the analyses. Breast-bands of Bar-throated Apalis consist of black, melanized feathers and breast-band size is thus not influenced by the abrasion of feathers.

Eggs were weighed within 1 day of egg-laying to the nearest 0.01 g using a portable TFT-100 digital balance. Laying date of first egg is expressed as Julian date counted from 1 July. Many clutches were predated before clutch completion and total clutch size of completed clutches was known for 31 nests of 15 pairs (mean: 2.8 ± 0.4 sd eggs). Among these pairs, each laid 3.4 ± 1.9 clutches during the study period. Replacement clutches (up to six) are commonly produced after a predation event, most of which were initiated within 9 days ($n = 36$ clutches) of nest failure.

Androgen assays

Thirty-nine eggs from 19 first clutches (clutch size: 2.1 ± 0.7 eggs) were collected on the third day after the clutch was initiated. This is unlikely to have had an important effect on the breeding population of Bar-throated Apalis given the very high predation rates at our study site (daily nest predation rates can reach 10.7% among ground- and shrub-nesting species of birds; Nalwanga *et al.* 2004a,b) and the frequency of replacement clutches laid after predation. There was no indication that nest visits by the researchers increased the likelihood of predation, because predation rates appear largely consistent and high across years at our study site, whereas research and nest monitoring intensity vary. Additionally, a host of predatory species predate in a largely random manner across bird species and nests, with nest concealment being the best predictor of the likelihood of predation (Nalwanga *et al.* 2004a,b). Incubation commences only once the clutch is

completed. Eggs were stored at $-18\text{ }^{\circ}\text{C}$ in the field and subsequently at $-80\text{ }^{\circ}\text{C}$ in the laboratory until yolk A4 and T concentrations were determined using radioimmunoassay. Yolks were weighed to the nearest 0.001 g after pouring out the albumen and removing any excess liquid. Steroid concentrations were determined using androgen-specific I-125 kits (A4: DSL-3800; T: DSL-4000; DSL, Webster, TX, USA) with an assay sensitivity of 0.03 ng/mL and 0.08 ng/mL for A4 and T, respectively. All samples were analysed twice in a single radioimmunoassay with intra-assay coefficients of variation of 8% for A4 and 4% for T.

Female nest attentiveness and male provisioning

To measure mate-feeding rates and their effect on female nest attentiveness, 13 nests, each of a different pair, were recorded on video at least once during incubation for a period of 3 h 58 min \pm 36 min (mean \pm sd; range: 1 h 35 min to 4 h 6 min; only one recording lasted for < 4 h due to adverse weather). Clutch size was three eggs at all 13 nests. One of these nests held the first clutch of that pair, while the remaining 12 contained second or subsequent clutches. Nests were filmed at 3.7 ± 3.8 days after the start of incubation ('incubation stage'; range: 1–16 days), and at five nests the video-recording was repeated at 9.8 ± 2.2 days after commencement of incubation (range: 8–13). This variability in the stage at which incubation and mate-feeding were filmed was due to logistics. Incubation stage, however, did not influence our results (see Results). Additionally, restricting our analyses to nests that were filmed between day 1 and 5 did not qualitatively change the results we report here. The 13 nests video-recorded to determine mate-feeding rates and female nest attentiveness were different from those nests used for yolk androgen assays. All video recordings were started within 1 h after sunrise and only on clear days to standardize environmental conditions. Nest attentiveness was defined as the percentage of time per hour that a female spent incubating at the nest, calculated as the total time spent incubating divided by the total time of observation. The number of times the male fed the female, prey size (estimated in beak lengths) where visible, and total amount of food (average prey size times number of feeds) delivered were determined.

Statistical analyses

One outlier (female body mass = 15.29 g) was removed from all models including female body mass to achieve normality (mean female body mass of all other females = 11.99 ± 0.55 g sd). Inclusion of the outlier in these models did not qualitatively change the results we report here. General linear models were used to assess whether female body mass was predicted by female breast-band size, with female tarsus length fitted as a covariate, or by male breast-band size, with male tarsus length fitted as a covariate. We used Spearman's rank correlation coefficient to test whether male and female breast-band size were correlated. Linear mixed models (LMMs) implemented using the package nlme in R (R Core Team 2011) with pair identity as a random factor were used to test whether male or female breast-band size predicted male provisioning frequency and the amount of food delivered by males to incubating females, and whether the amount of food delivered by males or male breast-band size predicted female nest attentiveness. For these analyses, male provisioning frequency was log($x + 1$)-transformed and the amount of food delivered square root-transformed to achieve normality. We used a linear regression model to determine the relationship between male and female breast-band size and egg mass using the means of egg mass per clutch, averaging across multiple clutches per female (3.44 ± 1.86 clutches per female, clutch size: 2.5 ± 0.72 eggs). Separate models were created for each sex to reduce the number of variables in each model, and laying date was included as a covariate. To assess how egg mass and composition change over the laying sequence, and to identify male or female traits that predicted yolk androgen concentrations, we used LMMs. Yolk mass was squared, yolk T concentration was square root-transformed and yolk A4 concentration log-transformed to achieve normality of the residuals of the LMMs. Breast-band size was square root-transformed prior to analyses to achieve normality, where appropriate. We used corrected Akaike information criterion (AICc)-based best-fit model selection with the function ' dredge ' from the ' MuMIn ' package in R (Barton 2013), which included intercept-only models, and $\Delta\text{AICc} < 2$ as the model selection criterion. AICc values were calculated using maximum likelihood. Model averaging was applied when more than one

Table 1. Morphological measurements of male and female Bar-throated Apalis.

	Males			Females		
	Mean \pm sd	CV	<i>n</i>	Mean \pm sd	CV	<i>n</i>
Breast-band size (mm ²)	130.15 \pm 38.67	0.29	22	81.11 \pm 33.74	0.42	18
Body mass (g)	11.67 \pm 0.38	0.03	21	12.16 \pm 0.93	0.08	19
Tarsus length (mm)	20.50 \pm 0.73	0.04	23	20.32 \pm 0.77	0.04	19
Body mass/tarsus length	0.57 \pm 0.03	0.05	21	0.60 \pm 0.05	0.08	19
Wing length (mm)	52.37 \pm 1.45	0.03	23	49.61 \pm 1.15	0.02	19

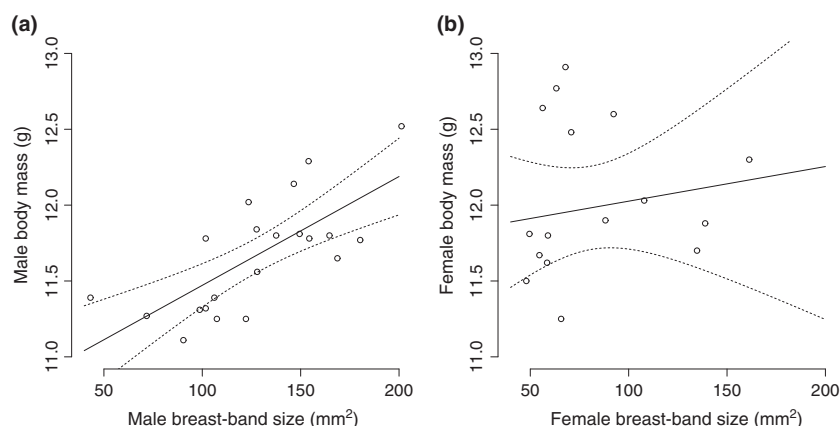
best-fit model was selected. We provide Δ AICc-values for the highest ranking subsets of the global models excluded from the best-fit models. Tarsus length was retained as a covariate in all models of male or female breast-band size to account for the effect of body size on breast-band size (Green 2001). Tarsus length, however, did not contribute significantly to any of these models ($P > 0.127$). Sample sizes vary between different models due to missing data. Statistical analysis was performed using R version 2.12.1 (R Foundation for Statistical Computing).

RESULTS

Morphological traits

Breast-band size in males and females was highly variable: in both sexes the coefficients of variation were substantially higher for breast-band size than for any of the other body-size measurements, including an estimate of body condition (body

mass/tarsus length; Table 1). Males had significantly larger breast-bands than females (Student's *t*-test; $t = 4.321$, 95% confidence interval (CI) = -3.565 to -1.289 , $P < 0.001$, $n = 40$). In males, body mass was predicted by breast-band size (model-effect estimate \pm se: 0.007 ± 0.002 , $r^2 = 0.529$, $t = 4.429$, $df = 18$, $P < 0.001$; Fig. 1), whereas in females no such association was found (-0.003 ± 0.005 , $r^2 = 0.129$, $t = 0.462$, $df = 14$, $P = 0.651$). Tarsus length was significantly associated with female breast-band size (28.550 ± 7.970 , $r^2 = 0.445$, $t = 3.583$, $df = 16$, $P = 0.002$) but not with male breast-band size (-1.851 ± 12.558 , $t = 0.147$, $df = 20$, $r^2 = 0.001$, $P = 0.884$). Finally, within breeding pairs, female body mass was not associated with male breast-band size (0.999 ± 0.944 , $r^2 = 0.045$, $t = 1.058$, $df = 9$, $P = 0.317$, $n = 12$), male and female breast-band size were not correlated (Spearman rank correlation; $S = 220$, $\rho = 0.396$, $P = 0.182$, $n = 13$), whereas male and female body mass tended to be positively correlated ($r = 0.598$, 95% CI -0.003 to 0.882 , $df = 9$, $P = 0.052$, $n = 11$).

**Figure 1.** Linear regression ($\pm 95\%$ CI) of (a) male and (b) female breast-band size over (a) male and (b) female body mass.

Breast-band size and paternal investment

Males fed incubating females 3.09 ± 4.43 (range: 0–15.57) times per hour of incubation time ($n = 18$), and prey delivered measured 1.15 ± 0.42 (0.5–2.0) beak lengths ($n = 12$). The amount of food delivered by the male averaged 3.70 ± 4.33 (0–13.61) units per hour of incubation time ($n = 14$). Male provisioning frequency was positively associated with male breast-band size (LMM; 0.063 ± 0.024 , $z = 2.276$, $P = 0.023$, $n = 16$; Fig. 2a) after model-averaging of the selected best-fit models (Table 2a). Time of the season was retained in the best-fit models but did not contribute significantly to the model after model averaging (0.096 ± 0.044 , $z = 1.554$, $P = 0.120$; Table 2a). Body mass, tarsus length and incubation stage were not retained in the set of best-fit models (Table 2a). However, the intercept-only model was among the best-fit models ($\Delta\text{AICc} = 1.23$), suggesting a low predictive value of any of the other variables included in the best-fit models. The amount of food delivered per hour of incubation time was also positively associated with male breast-band size (LMM; 0.027 ± 0.005 , $t = 4.931$, $df = 6$, $P = 0.003$, $n = 12$). Male tarsus length, male body mass and incubation stage were not retained in the single best-fit model (Table 2b). Female breast-band size was not retained in the single best-fit model predicting male provisioning frequency ($n = 15$; Table 2c) or in the best-fit model predicting the amount of

food delivered per hour ($n = 11$; ΔAICc of the highest ranking subset of the global model containing both female breast-band size and tarsus length = 12.07), which only contained the intercept-only model ($\text{AICc} = 38.6$). The other covari-

Table 2. Model selection table of competing models ($\Delta\text{AICc} < 4$) and the intercept-only model regarding paternal investment (subsets of the global model with $\Delta\text{AICc} > 4$ are not shown). Selected best-fit models with $\Delta\text{AICc} < 2$ are in italics, followed by ranked subsets of the global model. Weight is the AICc weight. Response variables are male provisioning frequency (a and c) and the amount of food delivered by the male (b).

Variables included	AICc	ΔAICc	Weight
(a)			
<i>Intercept, male breast-band size, time of the season</i>	93.0	0.00	0.277
<i>Intercept, male breast-band size</i>	93.6	0.64	0.201
<i>Intercept</i>	94.2	1.23	0.150
Intercept, male breast-band size, male body mass	96.0	2.96	0.063
Intercept, time of the season	96.4	3.40	0.051
(b)			
<i>Intercept, male breast-band size</i>	32.0	0.00	0.683
Intercept, male breast-band size, male tarsus length	34.4	2.48	0.197
Intercept	39.9	7.91	0.014
(c)			
<i>Intercept</i>	42.1	0.00	0.657
Intercept, female tarsus length	45.7	3.67	0.105
Intercept, female incubation stage	45.8	3.69	0.104
Intercept, female breast-band size	45.8	3.74	0.101

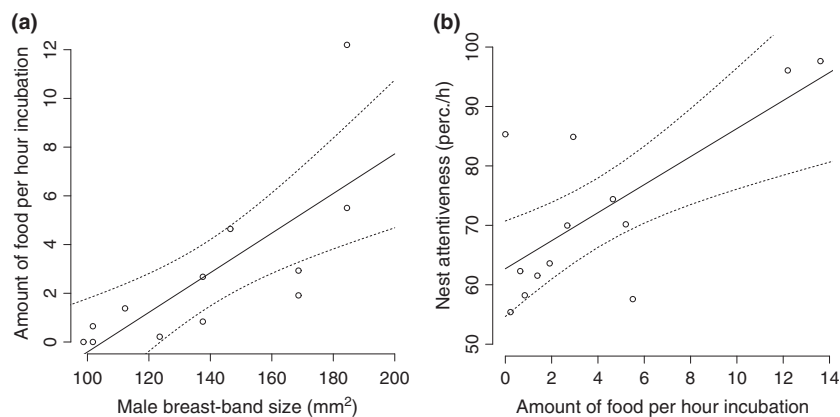


Figure 2. Linear regression ($\pm 95\%$ CI) of (a) the amount of food delivered by males to their mate per hour of incubation by the female in response to male breast-band size, and (b) nest attentiveness by the female in response to the amount of food per hour of incubation delivered by the male.

ates, i.e. female tarsus length and incubation stage, did not contribute significantly to these models predicting male provisioning frequency (Table 2c) and the amount of food delivered per hour ($\Delta\text{AICc} > 4.77$).

Breast-band size and maternal investment

The clutch size of 31 complete clutches among 15 pairs was 2.77 ± 0.50 (mean \pm sd) eggs. Clutch size was not related to male or female breast-band size, tarsus length, body mass or laying date (separate models for male and female traits; all $P > 0.162$) and none of these variables was retained after AICc-based model selection ($\Delta\text{AICc} > 2.69$) except for female body mass (P -value after model averaging = 0.162, $\Delta\text{AICc} = 0.84$). However, our AICc-based model selection could not distinguish between an intercept-only model ($\text{AICc} = 11.6$, $\Delta\text{AICc} = 0.00$) and the model containing female body mass and intercept ($\Delta\text{AICc} = 0.84$), and hence the predictive value of female body mass appears low.

Egg mass increased with male breast-band size but decreased with female breast-band size (Table 3, Fig. 3; variance inflation factor (vif) of female breast-band size = 1.516). Additionally, egg mass decreased with male and female tarsus length (Table 3; vif female tarsus length = 1.424). Laying date was negatively associated with egg mass in the model including female traits (Table 3b; vif = 1.228), whereas it was not retained in the best-fit model including male traits (Table 4a).

Table 3. Final linear regression model of mean egg mass per clutch (one clutch per pair) in response to (a) male ($n = 15$) and (b) female breast-band size ($n = 11$). Model averaging was used to calculate statistics for (b). Laying date and male body mass were not retained in the best-fit models after AICc-based model selection.

(a)	Model effect estimate \pm se	t	P
Male breast-band size	0.001 \pm 0.000	2.903	0.014
Male tarsus length	-0.091 \pm 0.026	3.452	0.005
(b)	Model effect estimate \pm se	z	P
Female breast-band size	-0.002 \pm 0.001	2.506	0.012
Female tarsus length	-0.004 \pm 0.001	2.493	0.013
Laying date	-0.159 \pm 0.049	2.786	0.005

Body mass was not retained in the best-fit models including either male or female traits (vif female body mass = 1.088; Table 4). The variance inflation factors reported here refer to the full linear regression model including female traits before model selection. A decrease in egg mass with female breast-band size could be due to more ornamented females producing more clutches. However, there was a negative, non-significant trend between female breast-band size and the total number of clutches produced (linear regression; -0.027 ± 0.013 , $t = 2.017$, $df = 8$, $r^2 = 0.194$, $P = 0.084$, $n = 10$), and there was no relationship between male breast-band size and the number of clutches produced by a pair (-0.004 ± 0.014 , $t = 0.274$, $df = 8$, $r^2 = -0.061$, $P = 0.792$, $n = 10$).

The concentration of T was not predicted by male breast-band size, which was not retained in our best-fit model, and only included the intercept ($\text{AICc} = 180.1$; ΔAICc of the highest ranking subset of the global model containing male breast-band size and tarsus length = 5.62). Laying date, male body mass, male tarsus length and laying order were also not retained in our final model ($\Delta\text{AICc} > 2.29$) and were not associated with the concentration of yolk T. Similarly, we found that the concentration of yolk T was not predicted by female breast-band size, which was not retained in our set of best-fit models (ΔAICc of the highest ranking model containing female breast-band size and tarsus length = 4.53), a model containing an intercept-only model ($\text{AICc} = 167.1$), a model containing the intercept and female tarsus length only ($\Delta\text{AICc} = 1.91$), or a model containing the intercept and laying date only ($\Delta\text{AICc} = 1.98$). Female body mass ($\Delta\text{AICc} = 2.08$) and laying order ($\Delta\text{AICc} = 2.65$) were also not retained in the best-fit models. Model averaging showed that female tarsus length (2.859 ± 3.041 , $z = 0.827$, $P = 0.408$) and laying date (0.071 ± 0.079 , $z = 0.807$, $P = 0.419$; $n = 26$ eggs) were not associated with the concentration of yolk T. Male breast-band size, male tarsus length, laying order and laying date were not retained in our final model and thus did not predict yolk A4 concentration ($\Delta\text{AICc} > 2.62$); only male body mass contributed significantly to a model predicting yolk A4 concentration ($\text{AICc} = 198.0$, 12.962 ± 4.425 , $t = 2.929$, $df = 12$, $P = 0.013$, $n = 27$ eggs; ΔAICc of intercept-only model = 5.19). Female body mass was also the only significant predictor of yolk

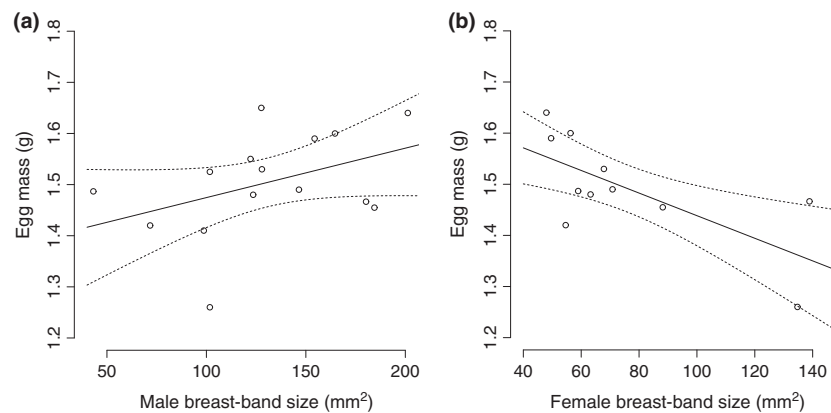


Figure 3. Linear regression ($\pm 95\%$ CI) of mean egg mass per clutch in response to (a) male and (b) female breast-band size.

Table 4. Model selection table of competing models ($\Delta AICc < 4$) and intercept-only model regarding mean egg mass per clutch in response to (a) male traits and (b) female traits (subsets of the global model with $\Delta AICc > 4$ are not shown). Selected best-fit models with $\Delta AICc < 2$ are in italics, followed by ranked subsets of the global model. Weight is the AICc weight.

Variables included	AICc	$\Delta AICc$	Weight
(a)			
<i>Intercept, male breast-band size, male tarsus length</i>	-26.9	0.00	0.522
Intercept, male tarsus length, male body mass	-24.3	2.62	0.141
Intercept, male breast-band size, laying date, male tarsus length	-23.1	3.83	0.077
Intercept, male tarsus length	-23.0	3.92	0.074
Intercept	-19.9	6.97	0.016
(b)			
<i>Intercept, female breast-band size</i>	-17.7	0.00	0.311
<i>Intercept, laying date, female tarsus length</i>	-17.5	0.17	0.285
Intercept, female tarsus length	-14.7	2.97	0.070
Intercept, female breast-band size, female tarsus length	-14.6	3.03	0.068
Intercept, female breast-band size, laying date	-14.5	3.16	0.064
Intercept	-14.4	3.30	0.060

A4 concentration in the model including female traits ($AICc = 191.4$, 5.062 ± 1.663 , $t = 3.045$, $df = 10$, $P = 0.012$, $n = 26$); all other variables, i.e. female breast-band size, female tarsus length, laying order and laying date, were not retained in the best-fit model ($\Delta AICc > 2.67$; $\Delta AICc$ of intercept-only model = 5.68).

Females spent $61.2 \pm 9.7\%$ of the day incubating ($n = 18$ females), averaging 1.78 ± 0.48 incubation bouts per hour, with each bout lasting

24.87 ± 10.19 min. The amount of food delivered by males was positively associated with female nest attentiveness (Fig. 2b; LMM; $AICc = 109.4$; 2.359 ± 0.709 , $t = 3.329$, $df = 3$, $P = 0.045$, $n = 13$). Incubation stage was not retained in this model after AICc-based model selection ($\Delta AICc = 4.67$; $\Delta AICc$ of intercept-only model = 4.73). We cannot exclude the possibility that this result is caused by males also feeding females away from the nest, so that females that spent more time incubating appeared to receive more food than females that were away from the nest more often, whereas in reality there may have been no difference in the amount of food received by females. However, we never observed males feeding females away from the nest. Nest attentiveness by the female was not predicted by male breast-band size: male breast-band size, male tarsus length and incubation stage were not retained in the final model.

DISCUSSION

The melanin-based breast-band of Bar-throated Apalises is a sexually dimorphic trait that may be used as a signal in inter-sexual communication. Breast-bands were larger in males than in females, yet highly variable in both sexes, making the breast-band a likely candidate as a quality signal upon which sexual selection may act (Dale 2006). Indeed, in males, but not in females, breast-band size correlated positively with body mass, suggesting that breast-band size is a reliable signal of male quality. Accordingly, we found that male reproductive effort (food provisioning to the female) and maternal investment (egg mass) were both predicted by male breast-band size, but also that

maternal investment was predicted by female ornamentation.

Our result that breast-band size predicts both male and female reproductive effort is consistent with the good-parent hypothesis (Hoelzer 1989) and with the differential-allocation hypothesis (Burley 1986, Sheldon 2000), both of which are likely to play a role in the reproductive behaviour and parental care of Bar-throated Apalis. First, as predicted by the good-parent hypothesis, females may select more ornamented males as mates if they are expected to provide better parental care. The latter is reflected in Bar-throated Apalis by increased mate provisioning during incubation by males with larger breast-bands, thus suggesting that the melanin-based male breast-band can signal direct benefits to females consistent with the good-parent hypothesis. We also found that mate provisioning was positively associated with female nest attentiveness, suggesting that a higher level of male provisioning allows the female to stay at the nest for more extended periods. We acknowledge that the reverse, i.e. more food delivered because the female stays at the nest for longer, might also be true, although it is difficult to reconcile this explanation with our result that male food provisioning increased with male breast-band size. Increased nest attentiveness is likely to influence embryonic development, growth efficiency and survival of offspring, and mate-feeding rates can thus have important fitness consequences (Olson *et al.* 2006, Martin *et al.* 2007). Surprisingly few studies have addressed mate-feeding rates in relation to male plumage characteristics and results are mixed. Examples include a positive relationship between courtship feeding and carotenoid-based plumage redness in House Finches *Haemorhous mexicanus* (Hill 1991), although the opposite was found in the same species in a later study (Badyaev & Hill 2002). In Eastern Bluebirds *Sialia sialis*, males with brighter blue structural plumage coloration achieved the highest provisioning rates (Siefferman & Hill 2005), whereas in Northern Cardinals *Cardinalis cardinalis* (Jawor & Breitwisch 2006) and in Great Tits *Parus major* (Matysiokova & Remeš 2010), neither carotenoid nor melanin signals of male quality predicted mate provisioning rates. Whether ornamentation can predict direct or indirect benefits and reproductive investment of male and female is thus likely to vary between species and environments and thus requires further detailed investigation. Our results suggest that

melanin-based ornaments of both sexes may predict reproductive investment of both males and females and are thus consistent with studies suggesting that melanin ornamentation is relevant in a reproductive context (Jawor & Breitwisch 2003, Bókony & Liker 2005).

Secondly, consistent with the differential-allocation hypothesis, female reproductive effort was positively associated with male ornamentation, as reflected by increased egg mass in relation to male breast-band size and increased nest attentiveness in relation to increased mate feeding by males with larger breast-bands. However, we found no evidence that yolk androgen concentration was associated with male ornamentation or body mass. Increased egg size as a result of differential allocation has been found to be more common in bird species with female-only care (Horváthová *et al.* 2012) and contradicts the notion that maternal investment and hormone allocation are used as a compensatory strategy for poor paternal care when paired with low-quality males, as found in the House Finch (Navara *et al.* 2006).

Females mated to males with large breast-bands may expect increased provisioning from their mates, as mate-feeding rates increased with male breast-band size. Such increased food availability, potentially including oxidative stress-reducing components, may allow for increased levels of circulating androgens in the female, as it is likely to help offset potential metabolic costs of elevated levels of circulating androgen concentrations in females (Alonso-Alvarez *et al.* 2008, Buttemer *et al.* 2010) and their offspring (Tobler *et al.* 2007, Tobler & Sandell 2009, Hall *et al.* 2010). This in turn allows for enhanced offspring competitiveness and growth (Alonso-Alvarez *et al.* 2007, Martin & Schwabl 2008, Moreno *et al.* 2013). Yolk hormone levels, in particular testosterone and dihydrotestosterone, have been shown to correlate with embryonic development rates as a response to ambient environment, including predation pressure, and therefore the need for rapid offspring development (Schwabl *et al.* 2007, Martin & Schwabl 2008). As predation pressure due to snakes, mongooses and avian predators is high at our study site (Nalwanga *et al.* 2004b), elevated levels of yolk androgens are likely to be beneficial for the offspring of Bar-throated Apalis, so it is therefore surprising that we did not find any evidence of a pronounced response to melanin

ornamentation in terms of yolk androgen concentration.

Although overall we found a positive association between breast-band size and reproductive effort, we also found that egg mass decreased with female breast-band size. However, unlike in males, female breast-band size was predicted by female tarsus length and female breast-band size may therefore merely reflect structural size variation. However, breast-band size in females was also highly variable compared with other structural traits, and female breast-band size might therefore convey information about individual females. One explanation may be that female breast-band size reflects the costs of circulating androgens, so that females with larger breast-bands have higher levels of circulating androgens, which may be reflected by increased androgen deposition in the eggs but may come at a cost in terms of egg mass (Bókony & Liker 2005). This association between melanin-based plumage and circulating androgens has previously been shown for males, but might be true for female ornamentation, too (Bókony *et al.* 2008). The link between melanin-based ornamentation, costs of elevated levels of androgens in adults and offspring, and fitness still requires research quantitatively testing whether female ornamentation is under direct sexual selection (Amundsen 2000, Amundsen & Pärn 2006) or is genetically correlated to selection on male ornamentation (Lande 1980, Fairbairn *et al.* 2007, Nordeide *et al.* 2013).

Taken together, we conclude that in the Bar-throated Apalis, male breast-band size is a reliable indicator of male quality and both male and female reproductive investment are associated with male and female breast-band size. However, we cannot distinguish whether potential benefits to females are a direct result of sexual selection for breast-band size or an indirect consequence of an association with a dominant male with a large breast-band holding a high-quality territory. Future experimental studies should focus on separating these possibilities.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Images illustrating a male Bar-throated Apalis with (a) a large and (b) a small breast-band.