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SHORT NOTE

Tail-racket removal increases hematocrit in male Turquoise-browed Motmots (*Eumomota superciliosa*)

Troy G. Murphy

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Abstract Graduated avian tails with short outer tail feathers and longer central tail feathers are thought to handicap aerodynamic function. The Turquoise-browed Motmot (*Eumomota superciliosa*) has a highly graduated tail with a long racket-tip that may impose a substantial aerodynamic cost. Previous research on this species has demonstrated a moderate sexual dimorphism in the tail, and has provided evidence that the racketed tail functions as a sexually selected trait only in males. To explore whether costs are associated with the maintenance of the ornamental male tail, I tested whether tail-racket removal affected hematocrit, a measure of condition and metabolic activity. I removed tail rackets from a manipulated group of males and left the rackets intact among a control group. I then compared change in hematocrit between the two groups over the breeding season. Males with rackets removed experienced a greater increase in hematocrit than did control males. This result suggests that males either experienced an increase in condition after being emancipated from bearing a costly sexually selected ornament, or that a social cost was associated with the loss of an ornament used in communication. This work supports previous research showing that the male tail functions as a sexual signal.

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T. G. Murphy
Department of Neurobiology and Behavior, Cornell University,
Ithaca, NY 14853, USA

Present Address:
T. G. Murphy (✉)
Department of Biology, Trinity University, San Antonio,
TX 78212, USA
e-mail: troy.murphy@trinity.edu

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Introduction

Much research has focused on the signal value of avian tails and the role of long tails in male sexual signaling (Andersson 1982; Winquist and Lemon 1994; Møller et al. 1998; Fitzpatrick 1999). Tail length is often the target of sexual selection because long tails can handicap normal aerodynamic function, and such costs can ensure signal honesty (Evans and Thomas 1992; Thomas 1993).

Based on aerodynamic models of Balmford et al. (1993), the avian tail aids flight by contributing lift and maneuverability. Lift is generated as the stream of air under the tail flows out around the outer edges and exerts an upward force on the underside of the tail. The length of the outer two tail feathers limits the part of the tail that generates lift, and any feathers beyond this are thought to create drag. Graduated tails (with short outer tail feathers and longer central tail feathers) represent one of the most aerodynamically costly tail shapes (Thomas and Balmford 1995). Because feathers outside the critical lift-generating area are unlikely to contribute aerodynamic benefits, these feathers are generally suspected to function as sexually selected traits (Balmford et al. 1993; Evans 2004).

Male and female Turquoise-browed Motmots (*Eumomota superciliosa*) have an extraordinary racket-shaped tail. The tail is graduated with long central tail feathers that extend far beyond the rest of the tail and terminate in large oval rackets. The tail is sexually dimorphic after controlling for differences in body size, and the wire (the barbless region of the central tail feathers; Fig. 1) is 10% longer in males (Murphy 2008). Research has demonstrated that sexually

Fig. 1 Racketed tail of the Turquoise-browed Motmot *Eumomota superciliosa*

selected benefits are associated with the male tail, but not with the female tail (female tails are thought to be maintained by natural selection for predator signaling; Murphy 2006, 2007a). Males with longer tail-wires have greater pairing success, pair with females that lay larger clutches, and have greater fledgling success (Murphy 2007b).

I tested whether the removal of tail rackets affected male hematocrit, a measure of the percent erythrocytes in the blood. Hematocrit is generally thought to reflect phenotypic condition (Amand 1986; Brown 1996; for review, see Fair et al. 2007) and an increase in hematocrit can indicate greater nutritional status (Bush 1975; Jones 1983; Campbell and Dein 1984; Dein 1986; Birkhead et al. 1998), and lower levels of bacterial infections (Coles 1997) and parasitism (Potti et al. 1999). In addition, animals can modify the concentration of erythrocytes to compensate for physiological demands for oxygen (Carpenter 1975; Palomeque and Planas 1978; Saino et al. 1997a), so an increase in hematocrit can also reflect greater metabolic activity (i.e., due to increased demands of provisioning, resource defense, etc.) (Saino et al. 1997b; Hõrak et al. 1998).

Methods

Eumomota superciliosa is a socially monogamous neotropical bird (Scott and Martin 1986) that breeds colonially in the Yucatan Peninsula of Mexico (Orejuela 1977; Murphy 2006). I studied motmots near the Ria Lagartos Biosphere Reserve in Northern Yucatan, Mexico (21°33′N, 88°05′W). Before breeding commenced in 2002, I captured and banded Motmots at two colonies (approx. 20 pairs each) separated by 0.7 km.

Early in the breeding season, I removed tail rackets from the two central tail feathers from a manipulated group of males and left the rackets intact among a similarly sized control group. I then recaptured birds later in the breeding season and compared the change in hematocrit within individuals. Hematocrit was measured by collecting blood from the brachial vein into a heparinized microhematocrit capillary tube (following methods of Campbell 1988). Each tube was centrifuged for 7 min in a portable centrifuge at 1,500*g*. Hematocrit was measured as the percent of blood cell volume to total volume within the capillary tube. Hematocrit was collected within 2 h of sunrise.

I captured birds and measured hematocrit before breeding commenced (initial capture at colony A: 4–23 April; at colony B: 2–18 May). Later in the breeding season, after birds had begun to feed nestlings, I recaptured birds from both colonies and measured hematocrit for a second time (second capture at both colonies: 15–19 July). The interval between the first measure and the second measure was approximately 80 days (mean ± SD = 80.2 ± 15.7).

The first individual captured was randomly assigned to an experimental group, and all subsequent birds were placed alternatively into experimental groups. In the manipulated group, I removed the rackets by cutting the two central rectrices at the proximal portion of the denuded feather shaft (i.e., the proximal wire). In the control group, I handled the birds in the same way, but did not cut their tails. Because the tail feathers were cut (instead of plucked), the feathers did not re-grow during the experimental period. All birds were sexed by laparotomy and there were no noticeable adverse effects of the procedure; laparotomized individuals were observed behaving normally the following day (see Murphy 2008). I only included adults (greater than or equal to second year of life) in the experiment, and age was assigned based on feather wear (unpublished data).

Statistical analyses were conducted using JMP v7.0.2 (SAS Institute, Cary, NC). Repeated measures ANOVA (rmANOVA) was used to test how the change in hematocrit varied by tail treatment. To control for the number of days each bird was in the experiment, the term ‘duration’ (date of second capture minus date of first capture) was included as a predictor in the model. Final sample size was reduced because I failed to recapture some birds and because some birds lost or damaged their tail during the experimental period (individuals excluded because not recaptured: control = 4, treatment = 1; because of lost or damaged tails: control = 1, treatment = 2). I additionally excluded individuals that failed to breed (birds that were not observed provisioning nestlings during two 3-h observation periods the week before recapture). Non-breeders were excluded because parent males invest substantially in provisioning nestlings, and such metabolic demands could affect hematocrit (excluded non-breeders: control = 2, treatment = 4). To test the validity of this assumption, an additional analysis was run on a data set that included non-breeders.

Results

At the start of the experiment, hematocrit did not differ significantly between manipulated and control groups (mean ± SE: racket removed = 42.2 ± 0.5, $n = 7$; control = 44.7 ± 1.4, $n = 7$; ANOVA: $F_{1,12} = 2.66$, $P = 0.13$). The initial measure of hematocrit did not differ significantly between colonies (mean ± SE: colony A = 44.7 ± 1.7, $n = 7$; colony B = 42.8 ± 0.9, $n = 7$; ANOVA: $F_{1,12} = 1.31$, $P = 0.27$), and initial hematocrit did not significantly correlate with date of measurement (least-squares: $F_{1,12} = 1.25$, $P = 0.29$). All individuals experienced an increase in hematocrit over the experimental period, probably due to the onset of the rainy season and increased availability of food. Racket-removed males experienced a significantly greater increase in hematocrit compared to control males (mean ± SE increase in hematocrit: racket removed 9.3 ± 1.5, $n = 7$; control 5.4 ± 0.8, $n = 7$; rmANOVA: model: $F_{2,11} = 5.6$, $P = 0.02$; duration: $P = 0.06$; tail treatment: $P = 0.038$) (Fig. 2). When non-breeders were included in the analysis, hematocrit did not differ significantly between manipulated and control groups; however, there was a trend for racket-removed males to experience a greater increase in hematocrit compared to control males (mean ± SE increase in hematocrit: racket removed 9.0 ± 1.0, $n = 11$; control 6.5 ± 1.1, $n = 9$; rmANOVA: model: $F_{2,17} = 5.2$, $P = 0.02$; duration: $P = 0.02$; tail-treatment: $P = 0.079$).

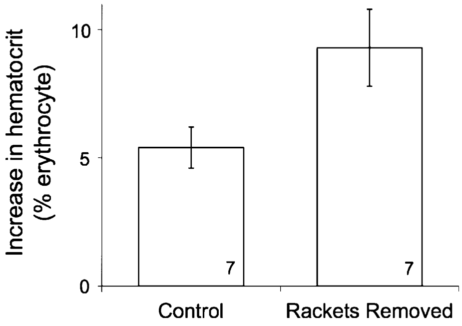

Fig. 2 Mean ± SE increase in hematocrit over an experimental period for two groups of birds: manipulated males with tail-rackets removed, and control males with intact tails. Sample size is shown at the bottom of each bar

Discussion

According to aerodynamic models of Balmford et al. (1993), the motmot's highly graduated and long racketed tail should be aerodynamically costly to maintain. I found that males with tail rackets removed experienced a greater increase in hematocrit compared to control males. The increase in hematocrit among racket-removed males suggests that these males increased their phenotypic condition after being emancipated from bearing a costly sexually selected ornament.

These results are similar to other studies that have shown a cost associated with elongate sexually selected tails. For example, Evans and Hatchwell (1992) showed that a reduction in the length of the elaborate pintail of the male Malachite Sunbird (*Nectarinia johnstoni*) increased efficiency of aerial foraging. Additionally, male Red-collared Widowbirds (*Euplectes ardens*) with shortened tails maintained elevated body condition compared to non-manipulated individuals (Pryke and Andersson 2005), and male Cape Sugarbirds (*Promerops cafer*) with shortened tails were found to have higher mean agility than those with unmanipulated tails (McFarlane 2006).

Although it seems reasonable to postulate that the Motmot's tail is aerodynamically costly, it is possible that the large increase in hematocrit experienced by racket-removed males can be partially explained because these males were deprived of their sexual/social means of communication, and so were forced to increased metabolic activity to counter social costs. Such costs could have arisen, for example, if males with removed tail rackets were rendered less effective at signaling status, and so were forced to invest more effort into competing for resources such as territories or food, or into defending their nest or mate. Alternatively, females paired to racket-removed males may have differentially allocated parental care based on the reduced attractiveness of their mate (sensu Burley 1988), and so males may have increased provisioning to compensate for this reduction. These interpretations are consistent with other studies that have shown that experimental reduction of sexual traits decreases ability to defend resources (Peek 1972; Evans and Hatchwell 1992; Pryke et al. 2002), and decreases investment in parental care by partners (Limbourg et al. 2004).

Despite small sample sizes, this manipulative study detected a significantly greater increase in hematocrit among racket-removed males compared to control males, and thus supports previous research showing that the male tail functions as a sexual signal. Future research on the function of the Turquoise-browed Motmot's tail should investigate aerodynamic costs to tail elongation, as well as how tail loss may affect social interactions both within and between the sexes.

Zusammenfassung

Die Entfernung der spatelförmigen Schwanzspitze erhöht den Hämatokritwert männlicher Brauenmotmots

Es wird angenommen, dass abgestufte Vogelschwänze mit kürzeren äußeren Schwanzfedern und längeren mittleren Schwanzfedern die aerodynamische Funktion behindern. Der Brauenmotmot (*Eumomota superciliosa*) hat einen stark abgestuften Schwanz mit einer langen spatelförmigen Spitze, die beträchtliche aerodynamische Kosten verursachen könnte. Bisherige Untersuchungen an dieser Art haben einen mäßigen Geschlechtsdimorphismus des Schwanzes gezeigt und Hinweise geliefert, dass der spatelförmige Schwanz als sexuell selektiertes Merkmal nur bei Männchen fungiert. Um zu untersuchen, ob mit der Aufrechterhaltung des zierenden Schwanzes der Männchen Kosten verbunden sind, habe ich getestet, ob das Entfernen der spatelförmigen Schwanzspitze den Hämatokritwert beeinflusste, ein Maß für Kondition und Stoffwechselaktivität. Ich habe die Schwanzspitzen von Männchen einer manipulierten Gruppe entfernt und den Schwanz bei einer Kontrollgruppe intakt gelassen. Dann habe ich die Veränderung im Hämatokritwert im Verlauf der Brutsaison zwischen den beiden Gruppen verglichen. Männchen, deren Schwanzspitzen entfernt worden waren, erfuhren einen stärkeren Anstieg im Hämatokritwert als Männchen der Kontrollgruppe. Diese Ergebnisse deuten darauf hin, dass Männchen entweder einen Anstieg der Kondition erfuhren, nachdem sie vom Tragen eines kostenintensiven sexuell selektierten Ornaments befreit worden waren, oder dass soziale Kosten mit dem Verlust eines Ornaments, das zur Kommunikation benutzt wird, verbunden sind. Diese Arbeit bestätigt vorherige Forschungen, die zeigten, dass der Schwanz der Männchen als sexuelles Signal fungiert.

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