Acrobatic Courtship Display Coevolves with Brain Size in Manakins (Pipridae)

Willow R. Lindsay   Justin T. Houck   Claire E. Giuliano   Lainy B. Day

Department of Biology, University of Mississippi, Oxford, Miss., USA

Abstract
Acrobatic display behaviour is sexually selected in manakins (Pipridae) and can place high demands on many neural systems. Manakin displays vary across species in terms of behavioural complexity, differing in number of unique motor elements, production of mechanical sounds, cooperation between displaying males, and construction of the display site. Historically, research emphasis has been placed on neurological specializations for vocal aspects of courtship, and less is known about the control of physical, non-vocal displays. By examining brain evolution in relation to extreme acrobatic feats such as manakin displays, we can vastly expand our knowledge of how sexual selection acts on motor behaviour. We tested the hypothesis that sexual selection for complex motor displays has selected for larger brains across the Pipridae. We found that display complexity positively predicts relative brain weight (adjusted for body size) after controlling for phylogeny in 12 manakin species and a closely related flycatcher. This evidence suggests that brain size has evolved in response to sexual selection to facilitate aspects of display such as motor, sensorimotor, perceptual, and cognitive abilities. We show, for the first time, that sexual selection for acrobatic motor behaviour can drive brain size evolution in avian species and, in particular, a family of suboscine birds.

© 2015 S. Karger AG, Basel

Introduction

Sexual selection for complex cognitive and behavioural skills has long been suspected to drive variation in brain size across animal taxa [Jacobs, 1996; Jerison, 1973; Lefebvre and Sol, 2008; Madden, 2001; Miller, 2000]. In humans, encephalization is thought by some to result from sexual selection for intelligence, related in part to the creative expression of motor activities such as tool use, hunting and even dance [Miller, 2000]. Indeed, brain size is related to motor behaviour across a wide subset of mammalian species [Changizi, 2003]. However, the role of sexual selection in linking brain size to motor behaviour lacks empirical support. In part, this may be due to a bias towards research on neurological specializations for sexually selected vocal portions of courtship display, predominantly in the oscine songbirds [Airey et al., 2000; Devoogd et al., 1993; Jarvis, 2006; Nowicki et al., 2002]. Few studies have examined avian brain specializations and in particular brain size in relation to physical, non-vocal elements of display despite the fact that these behaviours are at least as important as vocalizations for mate attraction [Byers et al., 2010].

Manakins (Pipridae) are lekking suboscine birds of the neotropics characterized by the production of visually striking acrobatic courtship displays [Prum, 1990, 1994]. In manakins, male reproductive success relies on female assessment of the male display [e.g. Barske et al., 2011; McDonald, 1989; Prum, 1997], with intersexual selection driving the evolution of physically elaborate behaviour

Willow R. Lindsay
Department of Biological and Environmental Sciences
Göteborg University, Medicinaregatan 18A, Box 463
SE–40530 Göteborg (Sweden)
E-Mail willowlindsay@gmail.com

Table 1. Species, sample sizes, and display complexity scores used in our analysis of brain weight by display complexity.

	n	Displays	Cooperation	Lekking	Arena	Mechanical	Complexity
M. vitellinus	3	10	1	1	3	9	24
M. candei	3	9	1	1	3	9	23
P. mentalis	6	8	1	1	1	10	21
P. cornuta	5	8	1	1	1	6	17
C. lanceolata	5	12	2	1	1	5	21
C. pareola	5	9	2	1	1	6	19
L. suavissima	3	9	2	1	2	5	19
L. coronata	3	11	2	1	2	0	16
C. altera	4	9	0	1	1	4	15
C. gutturalis	3	8	0	1	1	4	14
D. pipra	5	12	0	1	1	0	14
X. atronitens	4	3	0	1	1	7	12
M. oleagineus	4	7	0	1	0	0	8

The complexity score is the sum of: (1) displays: 40 possible discrete display traits [Castro-Astor et al., 2007; Chapman, 1935; Day et al., 2006; Duraes, 2009; Duval, 2007; Fusani et al., 2007a; Prum 1990, 1994; Rosselli et al., 2002; Skutch, 1949; Tello, 2001; Théry, 1990; Westcott and Smith, 1994; unpubl. observation] (see online suppl. table 1); (2) cooperation: 0 = none, 1 = simple (males display at the same time but not in concert), 2 = complex (the male display is coordinated) [Prum, 1994]; (3) lekking: 1 = yes, 0 = no; (4) display arena type: 1 = one or more horizontal perches or a fallen log, 2 = a loosely organized court near the ground composed of a few horizontal and vertical perches but without cleared ground, 3 = a true court with a cleared display arena [Prum, 1990], and (5) mechanical sound production: total repertoire (0–5), pulse type: 1 = single, 2 = single and multiple pulses, where sounds are produced: 1 = perched, 2 = in flight, 3 = perched and in flight [Skutch, 1949; Castro-Astor et al., 2007; Prum, 1998; Bostwick and Prum, 2003; unpubl. observation] (see online suppl. table 1).

[Prum, 1990, 1997, 1998; Snow, 1963]. Display behaviour varies across manakin species in terms of the complexity of acrobatic sequences and sonations, the degree of cooperation between displaying males and the amount of construction involved in preparing the display site (table 1; fig. 1) [Bostwick and Prum, 2003; Prum, 1990, 1994, 1998]. Such behavioural complexity likely requires a range of motor, sensorimotor, perceptual, and cognitive skills [Barske et al., 2011; Bostwick and Prum, 2003; Coccon et al., 2012; Day et al., 2011; Prum, 1986; Rosselli et al., 2002; Schlinger et al., 2008, 2013; Théry, 1990; Trainer et al., 2002].

The production of high-speed acrobatic displays and accompanying sonations requires precise motor control [Bostwick and Prum, 2003; Schlinger et al., 2008, 2013]. In golden-collared manakins *(Manacus vitellinus),* females choose mates based on millisecond differences in the performance of postural display sequences [Barske et al., 2011], and males vary in terms of the timing of these display elements [Fusani et al., 2007b]. The discovery of specializations of both male motor control circuitry and female visual processing centres [Day et al., 2011] supports the idea that the manakin brain has been shaped by evolution to support both male performance and female assessment of courtship display [Day et al., 2011]. Enhanced spatial cognition may also be necessary for both choreographed use of the spatial structure within a display arena [Coccon et al., 2012; Fusani et al., 2007b] and spatial navigation between alternate arenas [Prum, 1986; Rosselli et al., 2002; Théry, 1990]. Removal of a single perch in a golden-collared manakin's display arena reduces display quality [Coccon et al., 2012] and in white-throated *(Corapipo gutturalis)* and white-ruffed manakins *(C. altera),* males can display on multiple arenas separated by upwards of 350 m [Prum, 1986; Rosselli et al., 2002; Théry, 1990]. The role of practice and learning in the production of manakin displays remains undetermined but evidence from studies of two species, i.e. the golden-collared manakin and the long-tailed manakin *(Chiroxiphia linearis),* supports the idea that at least some display elements require experience to attain expert performance [Coccon et al., 2012; Trainer et al., 2002]. Combined, this evidence suggests that an array of cognitive skills is necessary for the performance of a manakin display, likely requiring the involvement of multiple brain regions.

While the courtship behaviour of many manakin species has been well documented, the neural mechanisms

enabling such behavioural complexity have only been studied in one species. In the golden-collared manakin, the skills necessary for the performance of a complex acrobatic courtship display are associated with specializations of the neuromuscular and neuroendocrine systems [Feng et al., 2010; Fuxjager et al., 2012a, b, 2013; Saldanha et al., 2000; Schultz et al., 2001; Schultz and Schlinger, 1999] and are reflected by predictable sex differences in the perception and sensorimotor regions of the brain [Day et al., 2011]. Thus, selection based on courtship display has profound impacts on the neural phenotype in at least one species of manakin [Day et al., 2011; Schultz and Schlinger, 1999]. Specializations of multiple brain nuclei have likely contributed to the variability of elaborate display behaviours across manakin species. Thus, sexual selection for motor display complexity is likely to be associated with increases in manakin brain size.

In only one family of birds, i.e. the oscine bowerbirds (Ptilonorhynchidae), has an association between sexual selection, a complex non-vocal courtship display and brain size been demonstrated. In bowerbirds, species that construct more complex courtship bowers have larger brains [Madden, 2001]. This appears to be related to both cognitive and motor behaviours as male bowerbirds that perform better in motor-dependent cognitive tasks have greater reproductive success [Keagy et al., 2011, but see Isden et al., 2013] and bower complexity is related not only to large brains but also specifically to expansion of the cerebellum [Day et al., 2005], a brain region involved in coordination and motor planning.

These findings relate specifically to the construction and decoration of an external display arena, i.e. the bower – they do not account for contributions of sexually selected motor behaviours such as male courtship dance. Additionally, no study to date has examined the relationship between sexually selected motor behaviours and specializations of the brain in a suboscine species. Here we used a comparative analysis to test the hypothesis that brain size has evolved to accommodate complex acrobatic motor display behaviours among manakin species.

Materials and Methods

Study Species and General Field Methods
We collected brain tissue and recorded the body weight of 53 adult breeding males of 12 species within the family Pipridae (table 1) and one member of the closely related Tyrannidae, i.e. the ochre-bellied flycatcher *(Mionectes oleagineus)*. Both the Pipridae and the Tyrannidae are suboscine birds belonging to the suborder Tyranni of the Passeriformes. Like the Pipridae, the ochre-bellied flycatcher has a lek breeding strategy with a courtship display [Westcott and Smith, 1994; Wolfson, 1952] and is primarily frugivorous. The ochre-bellied flycatcher is also sympatric with many of our target species.

We collected specimens between January and August (2012–2013) in Panama and Guyana. Golden-collared manakins, lance-tailed manakins *(C. lanceolata),* red-capped manakins *(Pipra mentalis),* blue-crowned manakins *(Lepidothrix coronata)*; and ochre-bellied flycatchers were captured near the Panama Canal in the region surrounding the small township of Gamboa, Panama Province, Panama (79°41′W, 9°07′N). We collected white-ruffed manakins in Parque Omar Torrijos, Coclé Province, Panama (80°38′W,

Fig. 1. Manakin displays and phylogenetic relationships, with one species per genus illustrated and similarities to congeners noted. **a** *X. atronitens:* a male performs a backflip including a wingsnap sonation [unpubl. observation]. **b** *C. lanceolata:* two males cooperatively perform a 'cart wheel' display in which each male flutters backwards over their partner, lands and hops up to take the other's place; only one male mates [Duval, 2007; Prum, 1990]. The *C. pareola* display is similar [Prum, 1990]. **c** *C. altera:* a male performs an 'above-the-canopy flight' followed by a plummeting 'log approach' with wing sonation; the male lands on the 'gardened' display log and performs a rapid 'about face' [Prum, 1990; Rosselli et al., 2002]. The *C. gutturalis* display is similar, with the addition of exposed throat ruff and white wing patches [Prum, 1990; Théry, 1990]. **d** *L. coronata:* a male performs swooping 'butterfly' or 'frenzied' flights between perches, with an aerial turn to land facing the opposite direction [unpubl. observation]; sometimes males 'bow' or perform an about-face pivot [Duraes, 2009]. The *L. suavissima* display is similar, with the addition of wing sonations and a 'slide-down' display performed on a vertical sapling [Théry, 1990; unpubl. observation]. **e** *M. vitellinus:* a male hops or flips between saplings and the ground on a cleared arena, loudly snapping his wings, lands with 'beard out', slides down a twig and produces a 'grunt' with the wings prior to copulation. **Inset** 'Rollsnap'; a series of rapid wing snaps are performed perched [Chapman, 1935; Day et al., 2006; Fusani et al., 2007a]. The *M. candei* display is similar [Prum, 1990]. **f** *P. mentalis:* a male swoops to a perch in an 'S' flight, quivers his tail and performs a 'moonwalk' by taking tiny backward hops, sometimes pivoting to moonwalk in the opposite direction. sometimes pivoting to moonwalk in a new direction [Prum, 1990; Skutch, 1949; Tello, 2001]. The *P. cornuta* display is similar, with a moonwalk performed by the execution of tiny backwards steps rather than hops [Tello, 2001; unpubl. observation]. **g** *D. pipra:* a male performs rapid jumps forwards and backwards on the display perch, and rapid 'to-and-fro flights' between perches [Castro-Astor et al., 2007; Prum, 1990; unpubl. observation]. **h** *M. oleagineus*: a male performs a simple display with frequent single wing lifts or 'flicks', 'hops' between perches and undulating flights similar to manakin butterfly flights [Westcott and Smith, 1994].

(For figure see next page.)

8°41′N), and white-collared manakins *(M. candei)* on the edge of the Sixaola River and Las Tablas Village, Bocas del Toro Province, Panama (82°44′W, 9°32′N). We captured white-crowned manakins *(Dixiphia pipra)* in the forests surrounding Surama Village and the Boro Boro River, Guyana (59°4′W, 4°8′N). Blue-backed manakins *(C. pareola)* were captured near the Rupununi River at the edge of Yupukari Village, Guyana (59°20′W, 3°39′N), and black manakins *(Xenopipo atronitens)* in the coastal savannah north of St. Cuthbert's Mission, Guyana (58°7′W, 6°22′N). Or-

ange-bellied manakins *(L. suavissima),* white-throated manakins, scarlet-horned manakins *(P. cornuta)* and ochre-bellied flycatchers were captured south of Kopinang Village in the Pakaraima Mountains, Guyana (59°53′W, 4°56′N).

We captured birds from active leks using mist nets. Sex and breeding conditions were confirmed by the presence of ejaculate after cloacal massage [Wolfson, 1952] and the presence and size of the testes. Birds were weighed to the nearest 0.1 g using a Pesola spring balance.

1
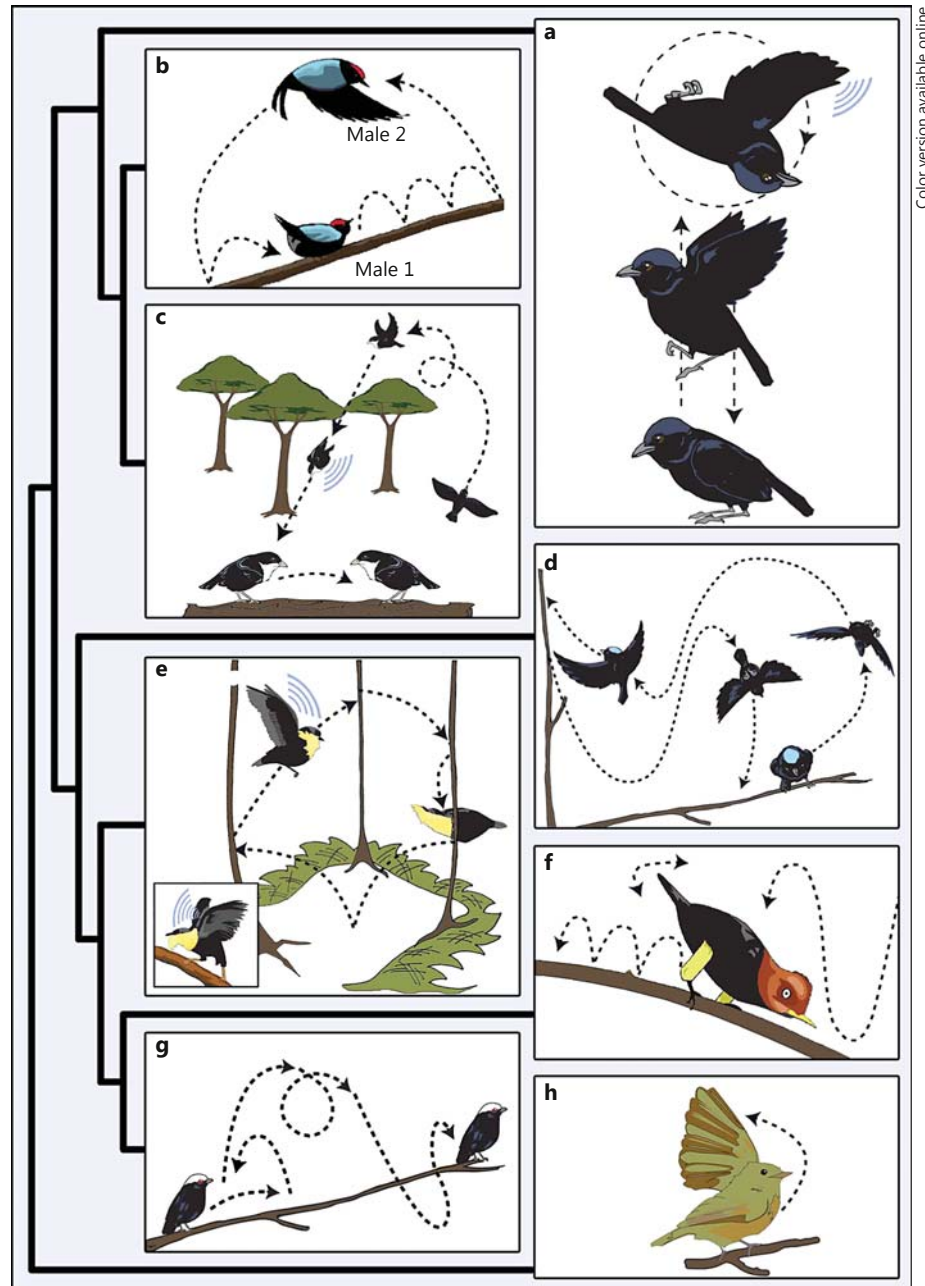
Tissue Preparation

Birds were anesthetized with isoflurane and perfused transcardially with phosphate-buffered saline followed by 10% neutral-buffered formalin. Perfused brains were dissected from the skull and weighed to the nearest 0.001 g.

Display Complexity

We produced a quantitative measure of display complexity based on the display character descriptions of Prum [1990], recently published ethograms of species courtship display behaviours [Castro-Astor et al., 2007; Chapman, 1935; Day et al., 2006; Duraes, 2009; Duval, 2007; Fusani et al., 2007a; Prum, 1994; Rosselli et al., 2002; Tello, 2001; Théry, 1990; Westcott and Smith, 1994] and behaviours documented by our own research team using high-definition and high-speed video and field observations (see online suppl. table 1; for all online suppl. material, see www.karger.com/doi/10.1159/000369244).

The total number of individually distinguishable motor sequences a bird can produce outside of the standard movements associated with perching and flight gives us the most objective measure of display possible [see similar scoring systems in Day et al., 2005; Madden, 2001]. Each species was given a numeric score based on the sum of assigned points (0 = absence, 1 = presence) for the production of all possible display characters (table 1; online suppl. table 1). Species behaviour was assessed for the production of discrete motoric elements of behavioural displays (e.g. performance of cartwheels, 'butterfly flights', hops, etc.; online suppl. table 1). We were careful to avoid redundancy in our counts by excluding characters with different names from different authors that described similar behaviours. We also quantified the level of cooperation expressed between males performing in a lek (from coordinated to uncoordinated) [Prum, 1994] as cooperation requires further motor coordination to synchronize movements between individuals, the type of arena utilized (from a cleared 'court' to a simple perch) [Prum, 1990] as this measures novel motor programs, and the capacity for production of high-speed sonations which each require distinct motor patterns [Bostwick and Prum, 2003; Prum, 1990, 1994] (for details on each category, see table 1). We have updated the earlier work of Prum [1998] to include recent findings on mechanical sound production in the Pipridae [Bostwick and Prum, 2003; Duval, 2007; Tello, 2001; unpubl. observation] (online suppl. table 1). Novel behaviours revealed by our observations include acrobatic display elements and mechanical sound production in *X. atronitens,* a species not previously thought to perform complex courtship displays [Sick, 1967], and other minor additions of elements for several species (online suppl. table 1). These discoveries include extensive field data and detailed descriptions that will be published separately.

Display complexity scores were calculated blind to brain weight data and were independently scored by 2 individuals using the resources cited above. Display complexity values were highly correlated between scorers (r = 0.899, p < 0.001).

Ethics Statement

All of our target species are common forest- or savannah-dwelling birds that form large, gregarious breeding groups, and none are listed as threatened or endangered. The Institutional Animal Care and Use Committee (IACUC) of the University of Mississippi approved our sampling procedures, and collections conducted in Panama were approved by the Smithsonian Tropical Research Institute IACUC and by the Autoridad Nacional del Ambiente and
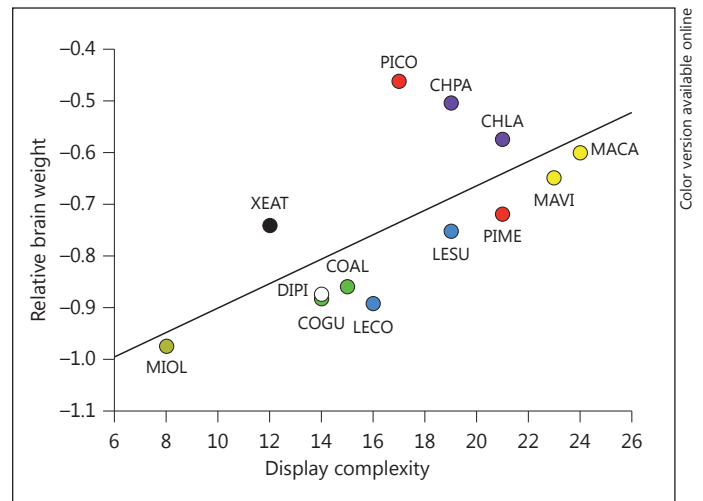

Fig. 2. Regression of relative brain weight after allometric correction for body size on complexity of reproductive courtship display for 13 suboscine species belonging to the Pipridae and Tyrannidae. The data presented in the figure does not control for phylogeny, unlike all analyses. Species data points are labelled with 4-letter abbreviations (MAVI = *M. vitellinus;* MACA = *M. candei;* CHLA = *C. lanceolata;* CHPA = *C. pareola;* PICO = *P. cornuta;* PIME = *P. mentalis;* LESU = *L. suavissima;* LECO = *L. coronata;* COGU = *C. gutturalis;* COAL = *C. altera;* DIPI = *D. pipra;* XEAT = *X. atronitens;* MIOL = *M. oleagineus*) and congeneric species pairs are depicted in similar colours/shades. Body size evolves faster than brain size, a fact that can confound the effects of selection on brain size even when allometric scaling is taken into account [Garcia-Pena et al., 2013]. *P. cornuta* was the largest of the manakin species in our comparative analysis, possibly explaining its elevated position in the regression presented here.

the Autoridad del Canal de Panamá. Collections conducted in Guyana were approved by the Guyana Environmental Protection Agency, and work conducted on Amerindian tribal lands was approved by the Guyana Ministry of Amerindian Affairs.

Statistics

Brain and body weight were positively correlated (p < 0.0001, $R^2 = 0.848$) across our 13 target species. We adjusted for this allometry by calculating the marginal means of brain size using a general linear model with log-transformed brain mass (mg) as the dependent variable, species as a fixed factor (n = 13), and log-transformed body weight (g) as a covariate. The resulting values were normally distributed (Shapiro-Wilk, p = 0.39) and were used in a subsequent analysis as our measure of body-size-adjusted relative brain weight. Our measure of display complexity was normally distributed (Shapiro-Wilk, p = 0.41).

We used a phylogenetic generalized least squares (PGLS) regression of brain size on display complexity to account for nonindependence of species data resulting from a shared common ancestry [Freckleton et al., 2002; Pagel, 1999]. PGLS regressions enable estimation of the phylogenetic scaling parameter λ, a measure of the phylogenetic dependence of trait covariance. We used likeli-

5

hood ratio tests to compare our model of trait evolution with a maximum likelihood estimate of λ to models where λ = 1 (strong phylogenetic association between variables) and λ = 0 (phylogenetic independence of trait covariance) [Freckleton et al., 2002]. We based our analysis on a 50% majority rule consensus tree generated using Geneious Pro 5.6 (Biomatters, Ltd.) from 10,000 trees of the 13 taxa downloaded from birdtree.org [see Jetz et al., 2012, for details on the methodology of tree construction] (see fig. 1 for genus level phylogeny). All species relationships and branch lengths are provided in nexus format in online supplementary table 2. Our consensus tree is consistent with other current avian phylogenies [Jetz et al., 2012; Ohlson et al., 2013].

Analyses were conducted using IBM SPSS Statistics 21.0 or the package 'caper' [Orme et al., 2013] in R 3.0.2 (R Core Team 2013). We visually validated model assumptions (normality of residuals and homogeneity of variance) for PGLS regression using model evaluation plots.

Results

We found that species variation in display complexity positively predicted species differences in relative brain weight (adjusted R^2 = 0.390, t = 2.944, p = 0.013, λ < 0.01; fig. 2). Our model with a maximum likelihood estimate of λ was not significantly different from one where λ was set to 0 (p = 1) or one where λ was set to 1 (p = 0.070), suggesting a very low phylogenetic signal in the determination of trait association.

Discussion

Brain size and the complexity of courtship behaviour have coevolved in manakins, likely as a consequence of sexual selection for acrobatic display. This is the first study, to our knowledge, to demonstrate a link between complex display behaviours and brain size in a group of suboscine birds, and it is the first study to indicate that selection for acrobatic motor behaviours in particular can drive brain size evolution in avian species. Relationships between sexually selected traits and brain size have been difficult to establish in other systems [Dechmann and Safi, 2009; Garcia-Pena et al., 2013; Guay and Iwaniuk, 2009; Lemaitre et al., 2009; Pitnick et al., 2006; Schillaci, 2006]. However, these studies have measured the association between brain size and sexual selected traits such as testes size [Dechmann and Safi, 2009; Garcia-Pena et al., 2013; Pitnick et al., 2006] and sperm competition [Guay and Iwaniuk, 2009; Lemaitre et al., 2009; Schillaci, 2006], traits that require no neural input. Our findings, along with those of Madden [2001], indicate that sexual selec-

tion may favour an increased brain size when the selected traits involved are behaviourally complex and would likely involve specializations of several brain regions.

Behavioural innovation and brain size are positively associated across avian and primate taxa [Lefebvre et al., 1997, 1998; Reader and Laland, 2002], with motor diversity predicting variations in problem-solving skills and the propensity to engage in novel behaviours [Griffin and Guez, 2014]. Thus, mate selection favouring an increase in manakin courtship display complexity may contribute to brain expansion via impacts on the rates of behavioural innovation and overall cognition functioning both within and outside the domain of courtship (e.g. foraging and predator avoidance). It is, however, unlikely that across-species variations in ecological and life history traits outside of motoric display behaviours explain our findings [see concerns in Dechmann and Safi, 2009; Healy and Rowe, 2007]. The species we examined differ in display behaviour but vary little in terms of non-display parameters that might alter the brain morphology such as developmental strategy, diet, group size, and habitat structure [Dunbar, 2010; Gonda et al., 2009; Iwaniuk and Nelson, 2001, 2003; Lefebvre et al., 1997, 2004]. Characters that do differ between our selected species do not mirror the structure of variation in display complexity. For example, no feeding innovations are documented for our target species [Lefebvre, pers. commun.], and territory size in the 10 species for which it is known does not increase with increasing display complexity [Prum, 1994; Théry, 1992].

Our findings on whole brain size and display complexity do not negate possible parallel relationships between regional brain specializations and display behaviour. Indeed, selection for the evolution of complex behaviour can lead to both brain enlargement and specializations of specific brain regions [Barton, 2008; Barton and Harvey, 2000; Finlay and Darlington, 1995]. For example, in the New Caledonian crow, innovations in tool use are associated with the evolution of relatively enlarged brains [Cnotka et al., 2008] as well as specializations of regions associated with the ability to memorize diverse stimuli and execute complex motor outputs [Mehlhorn et al., 2010]. In manakin species, specializations of motor control regions of the brain including the CB and arcopallium (AP) along with visual processing centres [Day et al., 2011] have likely enabled the evolution of such rapid and complex behavioural sequences and may contribute to the pattern of brain enlargement presented in this study. While the results presented here pertain only to the brains of male manakins, overall brain size is sexually monomorphic in the golden-collared manakin [Day et al.,

2011] despite predictable sex differences in various brain regions associated with sex-specific behaviours (specialized motor control regions in males vs. visual processing centres in females) [Day et al., 2011]. Therefore, variations in whole brain size may be species rather than sex specific across the Pipridae. Future comparative and experimental analyses should explore relationships between sexual selection for complex display, motor control and visual processing brain regions across manakin species and other species with complex motor displays.

While it is likely that selection on targeted discrete brain nuclei has contributed to our findings on whole brain size, developmental constraints on brain evolution due to the conserved nature of neural networks, energy demands and skull size may result in a coordinated brain expansion such that no regional specializations are detectable [Barton, 2008; Finlay and Darlington, 1995]. However, comparative analyses across multiple taxa increasingly show the capacity for independent evolution of brain regions despite the allometric effects of brain scaling [reviewed in Barton, 2008]. For example, such mosaic evolution explains the enlarged brains and CB of complex bower building bowerbirds without coordinated increases in the size of hippocampi [Day et al., 2005]. Further studies are needed to disentangle the contributions of regional expansion versus allometric scaling among brain regions to the pattern of increasing brain size with display complexity detected in this study.

Studies of sexually selected brain specializations in birds have largely focused on neural plasticity in song control circuitry expressed by members of the vocal learning suborder Passeri or oscine songbirds [Airey et al., 2000; Jarvis, 2006; Nowicki et al., 2002], while the brain plasticity of the non-vocal learning Tyranni or suboscines has been virtually ignored [but see Saldanha et al., 2000]. Our findings on the sexual selection of brain size in manakins are remarkable as they suggest that suboscine passerine brain evolution can be driven by sexual selection for motor complexity. This work will lead to continued research on the brain regulation of suboscine displays and will contribute to our understanding of how brain and motor systems can evolve in concert across vertebrate species.

References

Airey DC, Castillo-Juarez H, Casella G, Pollak EJ, DeVoogd TJ (2000) Variation in the volume of zebra finch song control nuclei is heritable: developmental and evolutionary implications. Proc Biol Sci 267:2099–2104.

Barske J, Schlinger BA, Wikelski M, Fusani L (2011) Female choice for male motor skills. Proc Biol Sci 278:3523–3528.

Barton RA (2008) Brain modules: mosaic evolution; in Squire L (ed): Encyclopedia of Neuroscience. Oxford, Academic Press, vol 2, pp 389–394.

Barton RA, Harvey PH (2000) Mosaic evolution of brain structure in mammals. Nature 405:1055–1058.

Bostwick KS, Prum RO (2003) High-speed video analysis of wing-snapping in two manakin clades (Pipridae: Aves). J Exp Biol 206:3693–3706.

Byers J, Hebets E, Podos J (2010) Female mate choice based upon male motor performance. Anim Behav 79:771–778.

Castro-Astor IN, Alves MAS, Cavalcanti RB (2007) Display behavior and spatial distribution of the white-crowned manakin in the Atlantic forest of Brazil. Condor 109:155–166.

Changizi MA (2003) Relationship between number of muscles, behavioral repertoire size, and encephalization in mammals. J Theor Biol 220:157–168.

Chapman FM (1935) The courtship of Gould's manakin (Manacus vitellinus vitellinus) on Barro Colorado Island, Canal Zone. Bull Am Mus Nat Hist 68:472–521.

Cnotka J, Gunturkun O, Rehkamper G, Gray RD, Hunt GR (2008) Extraordinary large brains in tool-using New Caledonian crows (Corvus moneduloides). Neurosci Lett 433:241–245.

Coccon F, Schlinger BA, Fusani L (2012) Male golden-collared manakins Manacus vitellinus do not adapt their courtship display to spatial alteration of their court. Ibis 154:173–176.

Day LB, Fusani L, Kim C, Schlinger BA (2011) Sexually dimorphic neural phenotypes in golden-collared manakins (Manacus vitellinus). Brain Behav Evol 77:206–218.

Day LB, McBroom JT, Schlinger BA (2006) Testosterone increases display behaviors but does not stimulate growth of adult plumage in male golden-collared manakins (Manacus vitellinus). Horm Behav 49:223–232.

Day LB, Westcott DA, Olster DH (2005) Evolution of bower complexity and cerebellum size in bowerbirds. Brain Behav Evol 66:62–72.

Dechmann DKN, Safi K (2009) Comparative studies of brain evolution: a critical insight from the Chiroptera. Biol Rev 84:161–172.

Devoogd TJ, Krebs JR, Healy SD, Purvis A (1993) Relations between song repertoire size and the volume of brain nuclei related to song – comparative evolutionary analyses amongst oscine birds. Proc Biol Sci 254:75–82.

Dunbar R (2010) Social brain: evolution; in Squire L (ed): Encyclopedia of Neuroscience. Oxford, Academic Press, vol 2, pp 21–26.

Duraes R (2009) Lek structure and male display repertoire of blue-crowned manakins in Eastern Ecuador. Condor 111:453–461.

Duval EH (2007) Cooperative display and lekking behavior of the lance-tailed manakin (Chiroxiphia lanceolata). Auk 124:1168–1185.

Feng NY, Katz A, Day LB, Barske J, Schlinger BA (2010) Limb muscles are androgen targets in an acrobatic tropical bird. Endocrinology 151: 1042–1049.

Finlay BL, Darlington RB (1995) Linked regularities in the development and evolution of mammalian brains. Science 268:1578–1584.

Freckleton RP, Harvey PH, Pagel M (2002) Phylogenetic analysis and comparative data: a test and review of evidence. Am Nat 160:712–726.

Fusani L, Day LB, Canoine V, Reinemann D, Hernandez E, Schlinger BA (2007b) Androgen and the elaborate courtship behavior of a tropical lekking bird. Horm Behav 51:62–68.

Fusani L, Giordano M, Day LB, Schlinger BA (2007a) High-speed video analysis reveals individual variability in the courtship displays of male golden-collared manakins. Ethology 113: 964–972.

Fuxjager MJ, Barske J, Du SM, Day LB, Schlinger BA (2012b) Androgens regulate gene expression in avian skeletal muscles. PLoS One 7:e51482.

Fuxjager MJ, Longpre KM, Chew JG, Fusani L, Schlinger BA (2013) Peripheral androgen receptors sustain the acrobatics and fine motor skill of elaborate male courtship. Endocrinology 154:3168–3177.

Fuxjager MJ, Schultz JD, Barske J, Feng NY, Fusani L, Mirzatoni A, Day LB, Hau M, Schlinger BA (2012a) Spinal motor and sensory neurons are androgen targets in an acrobatic bird. Endocrinology 153:3780–3791.

Garcia-Pena GE, Sol D, Iwaniuk AN, Szekely T (2013) Sexual selection on brain size in shorebirds (Charadriiformes). J Evol Biol 26:878–888.

Gonda A, Herczeg G, Merila J (2009) Adaptive brain size divergence in nine-spined sticklebacks (Pungitius pungitius)? J Evol Biol 22: 1721–1726.

Griffin AS, Guez D (2014): Innovation and problem solving: a review of common mechanisms. Behav Processes DOI: 10.1016/j.beproc.2014. 08.027.

Guay P, Iwaniuk AN (2009) Interspecific variation in relative brain size is not correlated with intensity of sexual selection in waterfowl (Anseriformes). Aust J Zool 56:311–321.

Healy SD, Rowe C (2007) A critique of comparative studies of brain size. Proc Biol Sci 274: 453–464.

Isden J, Panayi C, Dingle C, Madden J (2013) Performance in cognitive and problem-solving tasks in male spotted bowerbirds does not correlate with mating success. Anim Behav 86: 829–838.

Iwaniuk AN, Nelson JE (2001) A comparative analysis of relative brain size in waterfowl (Anseriformes). Brain Behav Evol 57:87–97.

Iwaniuk AN, Nelson JE (2003) Developmental differences are correlated with relative brain size in birds: a comparative analysis. Can J Zool 81: 1913–1928.

Jacobs LF (1996) Sexual selection and the brain. Trends Ecol Evol 11:A82–A86.

Jarvis ED (2006) Selection for and against vocal learning in birds and mammals. Ornithol Sci 5: 5–14.

Jerison HJ (1973) Evolution of Brain and Intelligence. New York, Academic Press.

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO (2012) The global diversity of birds in space and time. Nature 491:444–448.

Keagy J, Savard JF, Borgia G (2011) Complex relationship between multiple measures of cognitive ability and male mating success in satin bowerbirds, Ptilonorhynchus violaceus. Anim Behav 81:1063–1070.

Lefebvre L, Gaxiola A, Dawson S, Timmermans S, Rosza L, Kabai P (1998) Feeding innovations and forebrain size in Australasian birds. Behaviour 135:1077–1097.

Lefebvre L, Reader SM, Sol D (2004) Brains, innovations and evolution in birds and primates. Brain Behav Evol 63:233–246.

Lefebvre L, Sol D (2008) Brains, lifestyles and cognition: are there general trends? Brain Behav Evol 72:135–144.

Lefebvre L, Whittle P, Lascaris E, Finkelstein A (1997) Feeding innovations and forebrain size in birds. Anim Behav 53:549–560.

Lemaitre JF, Ramm SA, Barton RA, Stockley P (2009) Sperm competition and brain size evolution in mammals. J Evol Biol 22:2215–2221.

Madden J (2001) Sex, bowers and brains. Proc Biol Sci 268:833–838.

McDonald DB (1989) Correlates of male mating success in a lekking bird with male-male cooperation. Anim Behav 37:1007–1022.

Mehlhorn J, Hunt GR, Gray RD, Rehkamper G, Gunturkun O (2010) Tool-making New Caledonian crows have large associative brain areas. Brain Behav Evol 75:63–70.

Miller G (2000) The Mating Mind. London, Vintage.

Nowicki S, Searcy WA, Peters S (2002) Brain development, song learning and mate choice in birds: a review and experimental test of the 'nutritional stress hypothesis'. J Comp Physiol A Neuroethol Sens Neural Behav Physiol 188: 1003–1014.

Ohlson JI, Fjeldsa J, Ericson PGP (2013) Molecular phylogeny of the manakins (Aves: Passeriformes: Pipridae), with a new classification and the description of a new genus. Mol Phylogenet Evol 69:796–804.

Orme D, Freckleton RP, Petzoldt T, Fritz S, Isaac N, Pearse W (2013) Comparative analyses of phylogenetics and evolution in R. R version 0.5.2. cran.r-project.org/web/packages/caper/index.html.

Pagel M (1999) Inferring the historical patterns of biological evolution. Nature 401:877–884.

Pitnick S, Jones KE, Wilkinson GS (2006) Mating system and brain size in bats. Proc Biol Sci 273: 719–724.

Prum RO (1986) The displays of the white-throated manakin Corapipo gutturalis in Surinam. Ibis 128:91–102.

Prum RO (1990) Phylogenetic analysis of the evolution of display behavior in the neotropical manakins (Aves, Pipridae). Ethology 84:202–231.

Prum RO (1994) Phylogenetic analysis of the evolution of alternative social behavior in the manakins (Aves, Pipridae). Evolution 48:1657–1675.

Prum RO (1997) Phylogenetic tests of alternative intersexual selection mechanisms: trait macroevolution in a polygynous clade (Aves: Pipridae). Am Nat 149:668–692.

Prum RO (1998) Sexual selection and the evolution of mechanical sound production in manakins (Aves: Pipridae). Anim Behav 55:977–994.

Reader SM, Laland KN (2002) Social intelligence, innovation, and enhanced brain size in primates. Proc Natl Acad Sci USA 99:4436–4441.

Rosselli L, Vasquez P, Ayub I (2002) The courtship displays and social system of the white-ruffed manakin in Costa Rica. Wilson Bull 114:165–178.

Saldanha CJ, Schultz JD, London SE, Schlinger BA (2000) Telencephalic aromatase but not a song circuit in a sub-oscine passerine, the golden collared manakin (Manacus vitellinus). Brain Behav Evol 56:29–37.

Schillaci MA (2006) Sexual selection and the evolution of brain size in primates. PLoS One 1:e62.

Schlinger BA, Barske J, Day L, Fusani L, Fuxjager MJ (2013) Hormones and the neuromuscular control of courtship in the golden-collared manakin (Manacus vitellinus). Front Neuroendocrinol 34:143–156.

Schlinger BA, Day LB, Fusani L (2008) Behavior, natural history and neuroendocrinology of a tropical bird. Gen Comp Endocrinol 157:254–258.

Schultz JD, Hertel F, Bauch M, Schlinger BA (2001) Adaptations for rapid and forceful contraction in wing muscles of the male golden-collared manakin: sex and species comparisons. J Comp Physiol A 187:677–684.

Schultz JD, Schlinger BA (1999) Widespread accumulation of H-3 testosterone in the spinal cord of a wild bird with an elaborate courtship display. Proc Natl Acad Sci USA 96:10428–10432.

Sick H (1967) Courtship behavior in the manakins (Pipridae): a review. Living Bird 6:5–22.

Skutch AF (1949) Life history of the yellow-thighed manakin. Auk 66:1–24.

Snow DW (1963) The evolution of manakin displays. Proc Internat Ornithol Congr 13:553–561.

Tello JG (2001) Lekking behavior of the round-tailed manakin. Condor 103:298–321.

Théry M (1990) Display repertoire and social-organization of the white-fronted and white-throated manakins. Wilson Bull 102:123–130.

Théry M (1992) The evolution of leks through female choice: differential clustering and space utilization in six sympatric manakins. Behav Ecol Sociobiol 30:227–237.

Trainer JM, McDonald DB, Learn WA (2002) The development of coordinated singing in cooperatively displaying long-tailed manakins. Behav Ecol 13:65–69.

Westcott DA, Smith JNM (1994) Behavior and social-organization during the breeding-season in Mionectes oleagineus, a lekking flycatcher. Condor 96:672–683.

Wolfson A (1952) The cloacal protuberance: a means for determining breeding condition in live male passerines. Bird-Banding 23:159–165.