Phylogenetic constraint on male parental care in the dabbling ducks

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Phylogenetic constraint and inertia, i.e. limitations on future evolutionary trajectories imposed by previous adaptation, are often invoked to explain behavioural, morphological and physiological traits that defy explanation in an adaptive context. We reconstructed historical changes in male parental care behaviour in the dabbling ducks (family: Anatidae; tribe: Anatini) using a phylogeny based on mitochondrial DNA sequences. Male parental care is observed in many tropical and Southern hemisphere dabbling ducks but is lacking in all Northern hemisphere species. Southern hemisphere species that are very recently derived from Northern hemisphere ancestors, however, are exceptions to this general pattern. Lack of male parental care in these species can be attributed to phylogenetic constraint.

Keywords: adaptation; constraint; *Anas*; comparative analysis

1. INTRODUCTION

When the evolution of traits does not match the expectations of a scenario of adaptation, these traits are often described as being constrained (Gould & Lewontin 1979; Bell 1987; Wagner 1995; Podos 1997). Good empirical examples of phylogenetic constraint, however, are generally lacking (Schwenk 1995; Maynard Smith *et al.* 1985; McKittrick 1993). McKittrick (1993, p. 309) defined phylogenetic constraint as 'any result or component of the phylogenetic history of a lineage that prevents an anticipated course of evolution in that lineage'. Phylogenetic constraints or inertia may result from a lack of appropriate genetic variation for the origin of an adaptive trait or from a trade-off between an existing adaptation and the evolution of a novel adaptation that cannot be overcome with standing genetic variation (Wagner 1995; Maynard Smith *et al.* 1985). Such constraints may often result in an evolutionary lag between environmental change and the origin of a new adaptation. Here we explore the role of constraint on the evolution of male parental care in the dabbling ducks.

Among animal species, considerable variation exists in the kind and amount of parental care provided to offspring as well as in the relative contributions of males and females (Trivers 1972; Clutton-Brock 1991). A few workers have examined the evolution of parental care in a phylogenetic context (McKittrick 1992; Emerson 1996; Reynolds & Szekely 1997) yielding insights into the conditions that may favour the origin or loss of parental care strategies. While all female dabbling ducks invest

heavily in parental care (laying and incubating eggs then brooding, leading and defending ducklings), parental care by males is variable and associated with geographic distribution. Whereas males of all species in the Northern hemisphere desert their mates during incubation (Kear 1970), male behaviour in Southern hemisphere species is variable; males of some species provide parental care (in the form of leading and defending ducklings, Kear 1970; Siegfried 1974; Buitron & Nuechterlein 1989; McKinney & Brewer 1989; McKinney 1991), while males of other species desert the female. One possible explanation for behavioural variation among dabbling ducks from the Southern hemisphere is that environmental variation within the Southern hemisphere selects for different male strategies. However, species with alternative male parental care strategies can often be found breeding on the same ponds (McKinney & Brewer 1989), so environmental differences are unlikely to explain variation within the Southern hemisphere (unless there are other species-specific differences which alter the relative costs and benefits for parental care). This behavioural difference between closely related species in the same environment raises the possibility of constraint.

McKinney (1991) suggested that the general relationship between hemispheric distribution and male parental care in dabbling ducks could be explained by environmental factors and their influence on the length and timing of breeding seasons. Northern hemisphere ducks have a relatively short, synchronous breeding season each spring, and males presumably benefit by deserting the female during incubation and moving to moulting areas in preparation for autumn migration. This early departure from breeding areas precludes the evolution of male parental care. In contrast, breeding in the tropics and Southern hemisphere can occur over an extended period of time (tropics) or may be irregular and unpredictable

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(Southern latitudes). As a result, males may remain in the breeding area (i) to maintain long-term pair bonds (Kear 1970; McKinney 1991; Sorenson 1992), (ii) to engage in forced extra-pair copulations (McKinney *et al.* 1983) with females over an extended period (but see Sorenson 1992), and (iii) because their mates' breeding may be unpredictable (Siegfried 1974; Sorenson 1992; Sorenson *et al.* 1992). Remaining on the breeding area allows males to provide brood care and perhaps increase the survival of young. To test this 'breeding season hypothesis', we examined the evolution of male parental care in relation to breeding system, a binary character incorporating the length of breeding season, photorefractoriness and gonadal regression (Murton & Kear 1976).

2. METHODS

We scored species of dabbling ducks as either type A (long breeding season and absence of a photorefractory period and gonadal regression) or type B (short, seasonal breeding with a photorefractory period and gonadal regression at the end of the season) using Murton & Kear (1976). Most tropical and Southern hemisphere dabbling ducks have a type A breeding system, while type B is universally observed in Northern hemisphere species. We scored species as exhibiting male parental care or not from McKinney (1991, personal observation). We also scored species as breeding either in the Northern hemisphere or Southern hemisphere-tropics. We reconstructed changes in these characters over a mtDNA phylogeny (Johnson & Sorenson 1998) using MacClade (Maddison & Maddison 1992) with unordered parsimony. We tested the hypothesis that gains in male care occurred on branches with type A reconstructed (i.e. branches on which the character state type A for breeding system is inferred to be present using parsimony) using both the concentrated changes test (Maddison 1990) and contingent states test (Sillén-Tullberg 1993). We also determined whether changes in breeding system were associated with hemispheric distribution using the concentrated changes (Maddison 1990) and contingent states (Sillén-Tullberg 1993) tests.

To determine whether hemispheric distribution, breeding system and male parental care exhibit phylogenetic inertia in the dabbling ducks, we used the randomization procedure of Maddison & Slatkin (1991). We randomized observed character states to taxa 1000 times and determined if the observed number of steps in a character is shorter than the randomized distribution. To determine if evolutionary time-lags occur in changes in male parental care, we examined branch lengths (using the mtDNA data of Johnson & Sorenson (1998)) of taxa which did and did not fit the predicted pattern of male parental care in species with a type A breeding system. We calculated the average branch length of Southern hemisphere species with a type B breeding system to their nearest Northern hemisphere ancestors with type B and compared this to the average branch length for Southern hemisphere type A species to the nearest type B ancestors.

3. RESULTS AND DISCUSSION

Breeding system was significantly associated with geographic distribution (concentrated changes (Maddison 1990) and contingent states (Sillén-Tullberg 1993) tests; table 1, $p < 0.05$) suggesting an evolutionary response of breeding physiology to environmental conditions. In

Table 1. *Character state changes in contingent states tests for a set of reconstructions*

(a) hemisphere	reconstructed changes in breeding system			
	A to A	A to B	B to B	B to A
Southern	25	2	23	4
Northern	0	2	28	0

(b) breeding system	reconstructed changes in male parental care ^a			
	0 to 0	0 to 1	1 to 1	1 to 0
type A	14	7	8	0
type B	55	0	0	0

^a0, absent; 1, present.

addition, gains in male parental care occurred on branches with type A breeding system reconstructed, while losses occurred on branches with type B reconstructed, and the number of these associated changes was larger than expected by chance (Maddison 1990; Sillén-Tullberg 1993; $p < 0.015$, see figure 1 and table 1). These results suggest that differences in the length of breeding season influence the evolution of male parental care.

Although the breeding-season hypothesis is supported as an ultimate adaptive explanation for parental care in the dabbling ducks, exceptions to the overall pattern suggest an evolutionary lag in the breeding system and parental care in response to the invasion of new environments. The evolutionary responses of dabbling duck lineages that enter the tropics and Southern hemisphere conform to one of three basic patterns: (i) changes in both breeding season length and male parental care; (ii) change in breeding season only; and (iii) retention of both type B breeding and male desertion (figure 2). Type B breeding is conserved in two groups, 'blue-winged ducks' and 'mallards', that are distributed in both the Northern and Southern hemispheres. Both of these groups appear to have evolved relatively recently (within the last 1.3 million years using a rate of 2% sequence divergence per million years for mtDNA; Klicka & Zink 1997) based on branch lengths and genetic distances (see figure 3 for the mallards). The average branch length (number of DNA base changes) of Southern hemisphere species with type B breeding system to the nearest Northern ancestor with type B is 24.2 (range=0–47), while the average branch length for Southern hemisphere species with type A breeding system to the nearest ancestor with type B is 92.3 (range=5–143). Seven species of mallards and four species of blue-winged ducks live in the tropics or Southern hemisphere; however, only one of these 11 species (*Anas smithi*) has a type A breeding system. These observations suggest a time lag (phylogenetic constraint or inertia) in the evolution of new physiologies and behaviours in dabbling ducks colonizing the Southern hemisphere.

To examine the potential for phylogenetic inertia in breeding system, we analysed the phylogenetic information (Maddison & Slatkin 1991) in biogeographic distribution (Northern versus the tropics or Southern hemisphere) and breeding system (A versus B) by

Figure 1. (a) The presence and absence of male parental care is shown reconstructed (using MacClade; Maddison & Maddison 1992) over an mtDNA phylogeny of the dabbling ducks (Johnson & Sorenson 1998). White branches: male care absent; black branches: male care present; hatched branches: equivocal. There are three equally parsimonious reconstructions of equivocal branches. *A.*, *Anas*. (b) Breeding system (A or B) is shown reconstructed over the same phylogeny. White branches: type B; black branches: type A; hatched branches: equivocal. Asterisks denote species which are distributed in the tropics or Southern hemisphere but retain type B breeding system from the ancestral condition. There are two equally parsimonious reconstructions of equivocal branches. *A.*, *Anas*. Maddison's (1990) concentrated changes test and Sillén-Tullberg's (1993) contingent states test indicated that gains in male care occurred predominantly on branches with type A reconstructed and that losses in male care occurred predominantly on branches with type B reconstructed (for all possible resolutions of equivocal reconstructions, *p*-values ranged from 0.015 to < 0.001).

Figure 2. Types of transitions in breeding system and male parental care in dabbling ducks upon colonization of the Southern hemisphere. Only those patterns observed in the phylogeny are illustrated. Constraint is apparent upon invasion of the Southern hemisphere or tropics by the lag in the evolution of type A breeding system and male parental care. The lengths of the arrows are intended to represent the relative times since invasion of the Southern hemisphere.

comparing the actual number of changes in these characters to an expected distribution based on random assignment of character states to taxa. The breeding system contains significant phylogenetic signal ($p < 0.01$, i.e. shows many fewer steps than random assignments), but biogeographical distribution does not ($p > 0.10$). These results suggest phylogenetic inertia or constraint in the breeding system because it contains a phylogenetic component while the putative selective agent (environment and geography) is largely independent of phylogenetic history. In addition, the lack of association between breeding system and biogeographic distribution in some groups given the apparent adaptive changes in others is evidence that the 'expected course of evolution' is not observed in some of these very closely related lineages. Specifically, it may be relatively difficult to make a transition from a short breeding season with gonadal regression to a long breeding season with no gonadal regression.

Lack of appropriate genetic variation for hormone pathways involved in gonadal regression (Camper & Burke 1977) may be a mechanism that constrains the evolution of male parental care. Prolactin influences both gonadal regression and parental behaviour in birds (Camper & Burke 1977; Pederson 1989; Buntin 1996), and no species in the dabbling ducks with gonadal regression (type B) exhibits male parental care. In addition, Hahn *et al.* (1997) suggest that the transition from absolute photorefractoriness to temporal flexibility of reproduction may be difficult because of a lack of synthesis of cGnRH-1, a hormone critical for reproduction, during the photorefractory period in photorefractory species. These

Figure 3. Partial tree showing the relatively short molecular branch lengths in the mallard group versus other close relatives. Tree based on mtDNA sequences (Johnson & Sorenson 1998), with branch lengths proportional to the number of reconstructed base changes using ACCTRAN optimization. *A.*, *Anas*.

physiological considerations, together with the apparent time lag (see above), suggests that some factor (presumably lack of genetic variation or a physiological trade-off) prevents rapid evolution. The mallards are one group where phylogenetic constraint appears to be the strongest. Many mallard species are co-distributed with other dabbling duck species (some breeding on the same ponds) that exhibit male parental care and lack gonadal regression. However, no mallard species shows male parental care or gonadal regression. Inheritance of gonadal regression from a common ancestor and the recent radiation of this group based on phylogenetic branch lengths (figure 3) is suggestive of a constraint (McKittrick 1993) operating on these two adaptations.

The evolution of parental care behaviour in the dabbling ducks can be partially explained by an adaptive link between male desertion and a short breeding season. However, to fully understand the evolution of male parental care in this group, it is also important to understand evolutionary time-scales and the physiological mechanisms of breeding season length and parental behaviour. Recent changes in geographic distribution coupled with a lack of genetic variation in hormonal mechanisms may constrain the evolution of a potentially adaptive behaviour (male parental care) in some dabbling duck species. Both adaptation and phylogenetic constraint are important in the evolution of male parental care in the dabbling ducks.

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REFERENCES

- Bell, M. A. 1987 Interacting evolutionary constraints in pelvic reduction of threespine sticklebacks. *Biol. J. Linn. Soc.* **31**, 347–382.
- Buitron, D. & Nuechterlein, G. L. 1989 Male parental care of Patagonian crested ducks *Anas (Lophonetta) specularioides*. *Wildfowl* **40**, 14–21.
- Buntin, J. 1996 Neural and hormonal control of parental behavior in birds. *Adv. Stud. Behav.* **25**, 161–213.
- Camper, P. & Burke, W. 1977 The effect of prolactin on reproductive function in female Japanese quail (*Coturnix coturnix japonica*). *Poult. Sci.* **56**, 1130–1134.
- Clutton-Brock, T. H. 1991 *The evolution of parental care*. Princeton University Press.
- Emerson, S. B. 1996 Phylogenies and physiological processes: the evolution of sexual dimorphism in southeast Asian frogs. *Syst. Biol.* **45**, 278–279.
- Gould, S. J. & Lewontin, R. C. 1979 The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. Lond. B* **205**, 581–598.
- Hahn, T. P., Boswell, T., Wingfield, J. C. & Ball, G. F. 1997 Temporal flexibility in avian reproduction: patterns and mechanisms. *Curr. Ornithol.* **14**, 39–80.
- Johnson, K. P. & Sorenson, M. D. 1998 Comparing molecular evolution in two mitochondrial protein coding genes (cytochrome *b* and ND2) in the dabbling ducks (tribe: Anatini). *Mol. Phyl. Evol.* **10**, 82–94.
- Kear, J. 1970 The adaptive radiation of parental care in waterfowl. In *Social behavior in birds and mammals* (ed J. H. Crook), pp. 357–392. London: Academic Press.
- Klicka, J. T. & Zink, R. M. 1997 The importance of recent ice ages in speciation: a failed paradigm. *Science* **277**, 1666–1669.
- McKinney, F. 1991 Male parental care in Southern Hemisphere dabbling ducks. *Acta XX Congr. Int. Ornithol.* 868–875.
- McKinney, F. & Brewer, G. 1989 Parental attendance and brood care in four Argentine dabbling ducks. *Condor* **91**, 131–138.
- McKinney, F., Derrickson, S. R. & Mineau, P. 1983 Forced copulation in waterfowl. *Behaviour* **86**, 250–294.
- McKittrick, M. C. 1992 Phylogenetic analysis of avian parental care. *Auk* **109**, 829–846.
- McKittrick, M. C. 1993 Phylogenetic constraint in evolutionary theory: has it any explanatory power? *A. Rev. Ecol. Syst.* **24**, 307–330.
- Maddison, W. 1990 A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution* **44**, 539–557.
- Maddison, W. P. & Maddison, D. R. 1992 *MacClade: analysis of phylogeny and character evolution*. 3.04. Sunderland, MA: Sinauer.
- Maddison, W. P. & Slatkin, M. 1991 Null models for the number of evolutionary steps in a character on a phylogenetic tree. *Evolution* **45**, 1184–1197.
- Maynard Smith, J., Burian, R., Kaufman, S., Alberch, P., Campbell, J., Goodwin, B., Lande, R., Raup, D. & Wolpert, L. 1985 Developmental constraints and evolution. *Q. Rev. Biol.* **60**, 265–287.
- Murton, R. K. & Kear, J. 1976 The role of daylength in regulating the breeding seasons and distribution of wildfowl. In *Light as an ecological factor*, vol. 2 (ed. G. C. Evans, R. Bainbridge & O. Rackham), pp. 337–360. Oxford: Blackwell.
- Pederson, H. 1989 Effects of exogenous prolactin on parental behaviour in a free-living female willow ptarmigan *Lagopus l. lagopus*. *Anim. Behav.* **38**, 926–934.
- Podos, J. 1997 A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberizidae). *Evolution* **51**, 537–551.
- Reynolds, J. D. & Szekely, T. 1997 The evolution of parental care in shorebirds: life histories, ecology, and sexual selection. *Behav. Ecol.* **8**, 126–134.
- Schwenk, K. 1995 A utilitarian approach to evolutionary constraint. *Zoology (Jena)* **98**, 251–262.
- Siegfried, W. R. 1974 Brood care, pair bonds and plumage in southern African Anatini. *Wildfowl* **25**, 33–40.
- Sillén-Tullberg, B. 1993 The effect of biased inclusion of taxa on the correlation between discrete characters in phylogenetic trees. *Evolution* **47**, 1182–1191.
- Sorenson, L. G. 1992 Variable mating system of a sedentary tropical duck: the white-cheeked pintail (*Anas bahamensis bahamensis*). *Auk* **109**, 277–292.
- Sorenson, L. G., Woodworth, B. L., Ruttan, L. M. & McKinney, F. 1992 Serial monogamy and double brooding in the white-cheeked (Bahama) pintail. *Wildfowl* **43**, 156–159.
- Trivers, R. L. 1972 Parental investment and sexual selection. In *Sexual selection and the descent of man* (ed. B. Campbell), pp. 136–179. Chicago, IL: Aldine.
- Wagner, P. J. 1995 Testing evolutionary constraints hypotheses with early Paleozoic gastropods. *Paleobiology* **21**, 248–272.