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SHORT NOTE

Risky foraging leads to cost-free mate guarding in male teal *Anas crecca*

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Abstract Mate guarding by males is common in species with long-lasting pair bonds. We tested if the need to guard females affected foraging depth in male teal (*Anas crecca*), and if they were more vigilant than females when foraging with submerged eyes (preventing monitoring of competing males and predators). These predictions were not supported, suggesting that foraging depth selection is primarily driven by other factors, presumably food related. A likely reason why deeply foraging males did not increase vigilance is that 37.5% of the foraging time was already dedicated to it. The apparent lack of guarding costs in foraging male teal may explain why such small ducks can maintain pair bonds for up to 7 months.

Keywords Circumannual · Foraging behaviour · Mate guarding · Teal · Vigilance

Introduction

Many bird species form annual pair bonds long before nesting (e.g., Black 1996). Mate guarding by males is a common phenomenon in these species. This may affect daily time budgets for up to 7 or 8 months per year (e.g., Paulus 1983), not to mention species with lifelong monogamy, in which males may have to guard their mate throughout life (e.g. geese; Black et al. 1996). Consequently, mate guarding may have positive effects on fitness in both sexes in terms of natural as well as sexual selection. For males, this is often seen as a trade-off between vigilance, which reduces foraging efficiency, and enhanced breeding success, by sustaining the pair bond and preventing extra-pair copulations (e.g., Birkhead and Parker 1997).

Pairing in fall or early winter is considered to be adaptive in dabbling ducks *Anas* spp. (Hepp and Hair 1983), as mated birds get a dominant status within flocks that confers better access to food (e.g., Hepp 1986; Black 2005). This in turn allows paired females to improve body condition earlier than unpaired birds, which is likely to later translate into higher breeding success (due to the negative relationship between breeding date and success in *Anatidae*; Bowler 2005; Elmberg et al. 2005). However, precocial pairing also has drawbacks, especially for males; due to male-

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biased sex-ratios in duck populations (Baldassarre and Bolen 1994), males have to devote much time to guarding their female (e.g., Davis 2002; Guillemain et al. 2003). Male vigilance thus offers the female safer efficient foraging conditions, but is costly to males, if nothing else through reduced foraging efficiency.

In an earlier flyway-level study (Guillemain et al. 2006, in press), we observed that teal (*Anas crecca*) gradually increase foraging depth from September to August. This change is apparently due to predation risk restricting the behavioural repertoire in winter to safer shallow feeding methods, i.e., those with the eyes above the water surface (see also Guillemain et al. 2001). Conversely, the lower frequency of fly-overs by potential predators as the annual cycle progresses allows teal to use a wider variety of methods, including riskier deeper foraging when prey availability and energy requirements make it necessary. However, deep foraging with the eyes submerged not only limits the ability to detect predators, for a male it also prevents monitoring other males. Given (1) the costs of mate guarding, (2) that teal are paired for several months before breeding (e.g. Johnson and Rohwer 1998), and (3) the theoretically high relative energy requirements due to small body size compared to other dabbling ducks (ca. 300 g on average), we hypothesized that there should be intersexual differences in teal foraging behaviour.

Our aims were: (1) to determine if both sexes switch to deeper foraging methods over the annual cycle and, if so, if they do it at the same rate; alternatively, males may maintain vigilance by foraging shallower, e.g. by feeding on different food types than females, and (2) to test whether males and females partition foraging time into feeding bouts and interruptions in the same way when they rely on deep foraging. As deep foraging prevents monitoring of competing males, we hypothesized that deep foraging males should have shorter feeding bouts and/or longer foraging interruptions.

Study sites and methods are described in detail in Guillemain et al. (2006, in press). In brief, we used focal individual observations (Altman 1974) of foraging teal, chosen at random within flocks during daylight hours at 25 different sites in seven geographical areas within its flyway in western Europe (from Camargue in southern France to Västerbotten in north-central Sweden), covering the whole annual cycle except autumn migration stopovers. In total, 658 focal observations, i.e., the duration of ten successive foraging bouts using the same foraging method, plus the duration of the ten associated foraging interruptions, were recorded (244 females and 414 males). For each bird, we calculated an average value of bout length for foraging as well as for interruptions. Each foraging posture was associated with a feeding depth based on body measurements in Thomas (1982), e.g., bill length for dabbling, head + neck length for dipping, etc. Foraging depth does not necessarily depend on the depth of lakes, since ducks may also seek floating seeds and invertebrates in the water column. High turnover rates in teal assemblages (Pradel et al. 1997) made double recording of the same individual unlikely, with the possible exception of breeding lakes where density is low. Because each focal individual relied on one foraging method, associated with a certain depth, hence a discontinuous variable, means of behavioural parameters were computed for all birds per 10-day period (foraging depth and duration of foraging and interruption bouts).

We have earlier demonstrated that increased use of deep foraging methods from September to August is associated with a relaxation of predation risk (Guillemain et al. 2006, in press). Here, we do not address why birds change behavior, but rather use ANCOVAs to compare sex-specific patterns of mean foraging depth and duration of feeding bouts and interruptions over the year.

The model exploring mean foraging depth in relation to date and sex was significant ($F_{3,55} = 7.49$, $r^2 = 0.29$, $P = 0.0003$). However, neither sex nor sex × date had a significant effect (sex: $F = 0.03$, $P = 0.8539$; sex × date: $F = 0.08$, $P = 0.7792$). Instead, all variance was explained by date, i.e. foraging depth increased seasonally (10-day periods: $F = 21.37$, $P < 0.0001$; Fig. 1) at the same rate in both sexes, which on average foraged at the same depth.

For individuals foraging with submerged eyes, the model including sex, date, and sex × date did not fit with variation in average length of feeding bouts

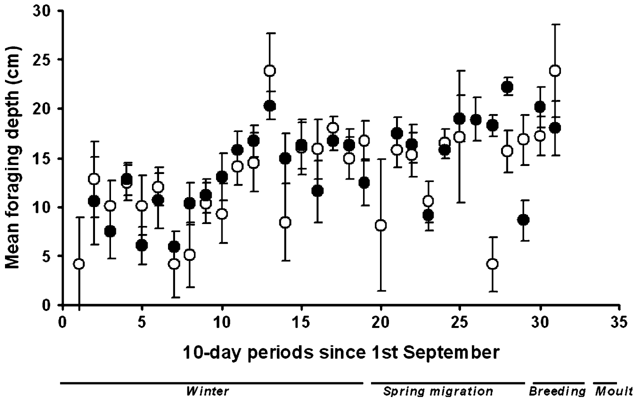

Fig. 1 Annual variation in foraging depth of male (*dots*) and female (*circles*) teal (*Anas crecca*) (mean ± SE), expressed per 10-day period starting 1–10 September. The main phases of the annual cycle are indicated under the *x*-axis. See main text for statistics

($F_{3.52} = 0.36$, $r^2 = 0.02$, $P = 0.7848$), nor feeding interruptions ($F_{3.52} = 1.35$, $r^2 = 0.07$, $P = 0.2682$). The partitioning of behaviour into foraging and vigilance thus remained unchanged over time, and did not differ between sexes when foraging in a posture preventing vigilance. Deep foraging bouts lasted 1.88 s on average (±0.09 SE, $n = 56$), feeding interruptions lasted 1.20 s (±0.06 SE, $n = 56$).

Among dabbling ducks, mate guarding has been shown to strongly influence male behavior in wigeon (*A. penelope*) (Mayhew 1987; Guillemain et al. 2003) and gadwall (*A. strepera*) (Dwyer 1975). Deeply foraging male teal cannot detect competing males, which is why we hypothesized that they should use this behaviour less than females do. However, this is not what we observed. Both sexes had similar foraging depths, and switched from shallow to deep foraging at the same rate over time. In a previous study, we hypothesized that relaxing predation risk over time would allow teal in general to increase foraging depth in response to higher energy requirements and/or changing food availability (Guillemain et al. 2006, in press). The latter factors may thus be more important than intrasexual competition to foraging depth selection in males or, alternatively, deep foraging is not as costly as hitherto assumed in terms of decreased ability to monitor competing males.

Our second prediction, i.e. that deeply foraging males unlike females alter their partitioning of behaviors by increasing vigilance, was not supported either. Average foraging bout length was similar (<2 s) between sexes, and interruptions lasted 1.2 s in both males and females. We suggest that deeply foraging males already have such high anti-predator vigilance (in terms of frequency of bouts as well as proportion of time) that they do not have to increase it further to guard their mate. As a comparison, male wigeon increased vigilance from 3.32 to 14.36% of foraging time after they paired (Guillemain et al. 2003). The corresponding percentage here is 37.5% for deeply foraging teal. This implies that, as opposed to earlier studies documenting high costs of mate-guarding, male teal do not pay a significant price for guarding their mate, at least when foraging. This may explain how such relatively small birds, with high relative energy requirements, can afford to form and defend pairs for up to 7 months a year (Johnson and Rohwer 1998).

Zusammenfassung

Riskante Nahrungssuche erlaubt männlichen Krickenten *Anas crecca* ein kostenfreies Bewacherverhalten

Bei Arten mit langer Paarbindung findet man bei den Männchen häufig ein Bewacherverhalten. Wir haben untersucht, ob die Notwendigkeit, die Weibchen zu bewachen männliche Krickenten (*Anas crecca*) in der Intensität der Nahrungsaufnahme beeinträchtigte, und ob sie bei der Nahrungssuche mit den Augen unter Wasser wachsamer waren als die Weibchen (um einer Überwachung konkurrierender Mänchen und Prädatoren vorzubeugen). Diese Hypothesen bestätigten sich nicht, was nahelegt, dass der Selektionsdruck auf die Intensität bei der Nahrungssuche primär von anderen, vermutlich an die Nahrung gekoppelten Faktoren angetrieben wird. Ein Grund, wieso intensiv nach Nahrung suchende Männchen ihre Wachsamkeit nicht erhöhten, liegt wahrscheinlich darin, dass 37.5% der Zeit auf Nahrungssuche bereits auf Wachsamkeitsverhalten verwendet wurde. Dass es bei Krickentenmännchen anscheinend keine Bewachungskosten gibt, könnte erklären, wieso diese kleine Entenart eine bis zu sieben monatige Paarbindung aufrecht erhalten kann.

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