

ARTICLE

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Adaptive significance of winter pair bond in male pintail, *Anas acuta*

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Abstract To test the female-advantage hypothesis that has been proposed to explain the adaptive significance of winter pair bonds in ducks, we examined the feeding and social behaviors of the northern pintail, *Anas acuta*. The female-advantage hypothesis assumes that male attendance offers paired females the benefits of increased social status and access to food, as well as less harassment from conspecifics, allowing them to spend more time feeding. Paired females dominated unpaired females, but neither time budgets of feeding nor frequency of feeding was significantly different between unpaired and paired females. The female-advantage hypothesis predicts that paired males spend less time feeding because they must closely guard their partners from harassment by male conspecifics. Paired males defended their mates by chasing and pecking the unpaired males. However, both time budgets of feeding and frequency of feeding were significantly higher in paired males than in unpaired males. Unpaired males frequently approached females while swimming. They performed courtship displays, mostly toward unpaired females. Paired males spent more time feeding by saving time and energy in courtship. We consider that the advantage of winter pairing for males comes from having a mate *plus* having an increase in feeding frequency.

Key words Adaptive significance · Winter pair bond · Northern pintail · Cost and benefit · Feeding and social behavior

Introduction

Pair bonds in many migratory birds are formed on the breeding grounds soon before reproduction (Oring 1982). It is only during the fertile period that the male guards the female to prevent cuckoldry (Birkhead and Møller 1992). Increasing sexual activity in both sexes is associated with increasing levels of gonadotropins and developmental changes in reproductive organs (Balthazart 1983). However, most ducks in the Northern Hemisphere do not exhibit this pattern. Pair bonds are typically formed between fall and winter on the wintering grounds (Oring and Sayler 1992). Despite undeveloped reproductive organs and low levels of gonadotropins, male ducks guard females and often copulate with them during winter (Höhn 1947; Donham 1979; Bluhm 1988).

Several hypotheses have been offered to explain the adaptive significance of pair formation during winter (Rohwer and Anderson 1988). A predominant hypothesis is the female-advantage hypothesis; i.e., male attendance offers paired females benefits of increased social status, access to food, increased protection from predators, and less harassment from conspecifics, affording more feeding time (Afton and Sayler 1982; Paulus 1983; Hepp and Hair 1984). An increase in feeding efficiency during winter is beneficial, especially for female ducks because they must obtain nutrient reserves on the wintering grounds to lay large clutches and large eggs requiring major lipid and protein acquisition (Alisauskas and Ankney 1992). Thus, if paired status increases feeding frequency and nutrient acquisition, selection should favor females that form pairs during winter.

Why then do male ducks form pair bonds during winter? The female-advantage hypothesis predicts that males suffer increased energy costs and elevated risks of mortality from attending females (Afton and Sayler 1982; Wishart 1983). If the costs of mate acquisition are offset by the gain other than mate acquisition, there would be an advantage to males of winter pairing. For example, if males can get the benefits of increased feeding efficiency (Wishart 1983), increase their own social status (Sorenson and

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Derrickson 1994), or synchronize body condition with females (Heitmeyer 1995) by forming pair bonds, selection may favor males forming pair bonds during winter. However, it is not yet clear that paired status is of material benefit to males.

To test the female-advantage hypothesis, we described the pairing chronology of the northern pintail *Anas acuta* (hereafter pintails) over the wintering season and examined the feeding and social behavior of individuals. Like many dabbling ducks, pintails form pair bonds, and the males guard their mates during winter (Johnsgard 1965; Miller 1985). We divided individual birds into four status types (unpaired male, paired male, unpaired female, and paired female) and compared their time budget of feeding, feeding frequency, distance moved while swimming, frequency of courtship, and aggressive behavior. If females gain benefits of increased feeding efficiency from being paired, paired females should spend more time feeding than unpaired females. If males suffer from increased energy expenditure by following mates, paired males should spend less time feeding and more time attacking other males. Inversely, if paired males increase their own social status and feeding efficiency by forming a pair bond, paired males should spend more time feeding than unpaired males.

Methods

Study area

Wintering pintails were studied on the Gohoden pond (36°20' N, 137°55' E, 523m elevation), located 14km northwest of Matsumoto City, central Japan, from October 1997 to March 1998. During the study period, waterfowl of six species (tundra swan, *Cygnus columbianus*; Eurasian wigeon, *Anas penelope*; pintail; common teal, *Anas crecca*; common pochard, *Aythya ferina*; and tufted duck, *Aythya fuligula*) wintered on the pond (~2.0ha of water surface area). At the pond, these waterfowl were provisioned three times a day (0800, 1200, and 1500) between October, when the swans first arrived, and March, when they left for Siberia. Thus, observations were not conducted for 1 h from the time when the extra food (rice seed) was supplied, because once the food was provided crowds of waterfowl assembled and began feeding excitedly.

Pairing chronology

We counted pintails using a 20× spotting scope. The sex of each bird (based on plumage) was noted on a tape recorder. While we were counting the number of birds, each female was observed for at least 10s and her pairing status was assessed. Those accompanying a male within 2m and exhibiting consistent synchronization of activities, especially swimming, were classified as “paired”; the remainder were considered “unpaired.” Based on the same criteria, we also classified males into “paired” and “unpaired.” Pairing chro-

nology was determined from the percentage of females judged to be paired. We put in a total of 2–4h per census and conducted the census at biweekly intervals.

Behavioral study methods

During 1 week, February 26 to March 4, the behavior of 16 unpaired males, 13 unpaired females, 24 paired males, and 24 paired females was recorded with a video camera (Sony; CCD-TR3300). During the recording, focal birds of each type were individually recognized by variations in plumage and bill characteristics. They were selected carefully to avoid choosing the same individuals more than once. The behavior of focal birds was continuously recorded during 0.5-h sampling periods randomly selected during daylight. Although birds were not marked, numbers of pintails were usually large enough to avoid repeated sampling.

We monitored feeding behavior, distances moved while swimming, courtship displays, and aggressive interactions. We calculated time budgets of feeding (percentage of time that individuals spent feeding) based on measurements of feeding time using an electronic stopwatch while viewing the tapes. Pintails took floating food by filter-feeding on the surface and took sinking food by submerging their necks or heads. It was easy to count the number of submergences for feeding. Thus, we calculated the frequency of submergence (per minute). A feeding bout was defined as an action that started when a focal individual lowered its bill or head into water to forage and ended when it raised its bill or head. Pintails swam to feed or seek mates. We measured the distance (m) moved while swimming (per minute). Distances were estimated using the body length of the bird as a scale.

Male pintails performed a variety of courtship displays as follows: head-pumping, chin-lifting, head-up-tail-up, grunt-whistle. Female pintails used “inciting” to simultaneously signal preference for one male and rejection of other males (Johnsgard 1965). We defined these displays of both sexes as a courtship bout. Courtship frequency was quantified by calculating the number of courtship bouts per minute of observation.

We observed 574 intraspecific aggressive interactions from a total of 38.5 h of observations. Some aggressive behavior was threatening, chasing, and biting (11% of 574), but most was pecking ($n = 511$, 89% of 574). Focal birds pecked conspecifics in 292 interactions, while they were pecked by conspecifics in 219 interactions. Thus, we calculated the frequency of both pecking and being pecked (per minute). The status type of focal birds involved in the peck interactions was recorded. A bird was said to be dominant to another when it pecked the other.

Statistical analysis

One-way ANOVA was used to determine significant differences of the frequency of behaviors among ducks of different status types. When ANOVA revealed significant differences among social types, post hoc differences be-

Fig. 1. Seasonal changes in number of pintails and pairing chronology of females during the winter of 1997–1998

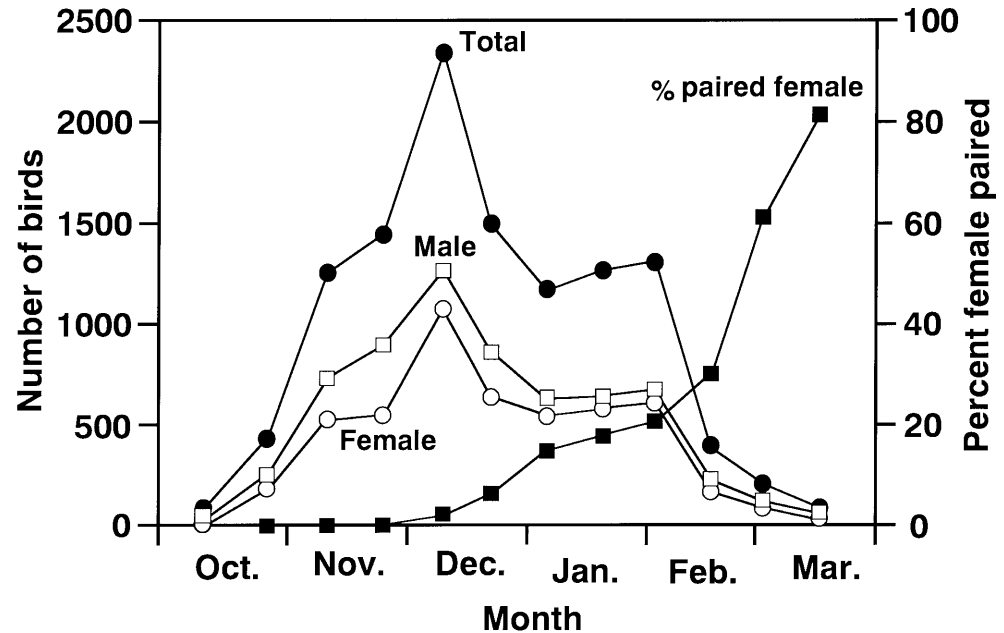


Table 1. Comparisons of the time budget of feeding, frequency of submergence, distance moved while swimming, frequency of courtship, and agonistic displays among unpaired and paired pintails

	Male			Female		
	Unpaired (16)	Paired (24)	<i>P</i>	Unpaired (13)	Paired (24)	<i>P</i>
Time budget of feeding (%)	3.62 ± 1.49	43.71 ± 6.16	<0.0001	59.92 ± 6.98	65.16 ± 4.91	=0.940
Frequency of submergence	0.14 ± 0.05	3.73 ± 0.78	<0.05	3.90 ± 1.15	4.03 ± 0.79	=0.999
Distance while swimming (m)	9.00 ± 0.93	4.67 ± 0.53	<0.001	5.77 ± 0.70	4.42 ± 0.55	=0.604
Frequency of courtship display	2.24 ± 0.51	0.40 ± 0.06	<0.0001	0.00 ± 0.00	0.13 ± 0.04	=0.982
Frequency of pecking	0.06 ± 0.02	0.33 ± 0.07	<0.05	0.16 ± 0.10	0.12 ± 0.04	=0.962
Frequency of being pecked	0.10 ± 0.02	0.10 ± 0.02	=0.999	0.24 ± 0.60	0.09 ± 0.03	<0.05

Data are mean ± SE (sample sizes in parentheses)

Frequency is the number of instances of a behavior per minute

Differences were tested using the Scheffe *F*-test

tween different types of pairs were assessed by the Scheffe *F*-test; the *G*-test was used to determine the dominance relationships between bird status types.

Results

Pairing chronology

Pintails began arriving in the study area in mid-October and left by late March (Fig. 1). The number of males and females increased gradually from October to December 9 but declined thereafter. The sex ratio of the population favored males (range, 53%–64%) throughout the study period (Fig. 1).

Males completed the prealternate molt by early November. The first pairs were seen on December 9. The proportion of paired females in the population increased steadily from December to mid-February and increased rapidly in

March (Fig. 1). By mid-March, the proportion of females paired approached 81%. We observed seven copulations, three in February and four in March.

Feeding behavior

There was a significant difference in the time budgets of feeding among the four duck status types ($F = 23.00$, $df = 3$, 73 ; $P < 0.0001$), with the budget in unpaired males being the lowest (Table 1; $P < 0.0001$ for each type). Unpaired and paired females spent about 60% and 65% of their time feeding, respectively, but the difference was not significant (Table 1).

One-way ANOVA showed a significant difference in the frequency of submergence among the four status types ($F = 4.89$, $df = 3$, 73 ; $P < 0.01$). That of unpaired males was the lowest of four types (Table 1; $P < 0.05$ for each type), but no difference in submergence was detected between unpaired and paired females (Table 1).

Distance moved while swimming

Distance moved while swimming varied significantly among the four status types ($F = 9.62$, $df = 3, 73$; $P < 0.0001$). The distance swum by unpaired males was the longest (Table 1; $P < 0.05$ for each type). There was no significant difference in the distance swum by unpaired and paired females (Table 1); this means that whether females were paired did not influence their swimming behavior. Once paired, males followed their mates. Therefore, we did not find a significant difference in the distance that paired males and paired females swam ($P = 0.993$).

Courtship frequency

The frequency of courtship display varied significantly among the four status types ($F = 20.06$, $df = 3, 73$; $P < 0.0001$). Males and paired females engaged in courtship displays, but unpaired males were most active (Table 1; $P < 0.0001$ for each status type). Unpaired males frequently approached females while swimming. They performed displays toward both unpaired and paired females, but mostly toward unpaired females (93% of 942 cases). Paired males directed courtship displays to their mates, as well as to other females, but most of them (92% of 225 cases) were toward their mates. If their own mate was courted, paired males usually defended their pair bond by chasing and pecking the rival males. Paired females performed incitements virtually only toward a nearby approaching male (97% of 87 cases).

Aggressive interaction

The frequency of pecking varied among the four status types ($F = 4.83$, $df = 3, 73$; $P < 0.01$). Paired males pecked more often than did unpaired males (Table 1) or paired females ($P < 0.05$). However, no difference was detected between unpaired and paired females (Table 1). The frequency of being pecked also varied among the four status types ($F = 4.23$, $df = 3, 73$; $P < 0.01$). Unpaired females were pecked more often than were paired females (Table 1) or paired males ($P < 0.05$). There was no significant difference between the remaining combinations ($P > 0.05$ for each combination).

Paired males dominated unpaired males more often than would be expected if paired and unpaired males were equal in dominance status (138 of 160 encounters; $G = 50.66$, $df = 1$, $P < 0.0001$). Similarly, paired males dominated unpaired females (47 of 58 encounters; $G = 12.70$, $df = 1$, $P < 0.001$). Paired females won 73% of contests with unpaired males ($n = 70$, $G = 7.81$, $df = 1$, $P < 0.01$) and 74% of contests with unpaired females ($n = 38$, $G = 4.58$, $df = 1$, $P < 0.05$).

Discussion

The female-advantage hypothesis assumes that male attendance offers paired females increased social status

and increased feeding efficiency. In our study, paired females dominated over unpaired birds and were pecked less by conspecifics (Table 1). However, we did not find a significant difference between paired and unpaired females in either time budgets of feeding or frequency of submergence (Table 1). This result means that male attendance does not increase the feeding frequency of paired females.

It is important especially for female pintails to increase feeding frequency and accumulate nutrient reserves on the wintering grounds. Esler and Grand (1994) recorded that female pintails exhibit the greatest reliance on lipid reserves among ducks during the formation of the first clutches (see also Mann and Sedinger 1993). Moreover, female pintails with larger reserves are able to nest earlier and lay larger clutches (Mann and Sedinger 1993; Esler and Grand 1994). Early nesting pintails have better nesting success and duckling survival (Grand and Flint 1996; Flint and Grand 1996). Thus, if females need nutrient reserves, they should devote all their energy to feeding whether they form pair bonds or not. Our results support this prediction. However, the female-advantage hypothesis cannot be dismissed in terms of protection from sexual harassment, because paired females were pecked less than unpaired females (see Table 1). Thus, paired females may be less stressed.

The female-advantage hypothesis also predicts that male attendance offers paired females the benefits of increased protection from predators. Pintails are vulnerable to predators while they take sinking food by submerging their necks or heads because their eyes are under water at that time. However, there was no significant difference in the frequency of submergence between unpaired and paired females (Table 1). This result suggests that the benefit of protection from predators is not essential for paired females. On the study pond, many waterfowl including pintails fed in flocks throughout the study period. Investment in vigilance usually decreases with increasing flock size (reviews in Elgar 1989; Lima and Dill 1990). It is reasonable that flock feeding, not pair feeding, gives pintails a vigilance profit (i.e., saving vigilance time watching for flying predators and having more time for feeding).

Most studies on the winter pair bond of ducks have emphasized the female advantages, while the male advantages have been underestimated. The primary benefit to males of winter pairing is mate acquisition. If males can form pair bonds with high-quality females (Wishart 1983), or bond with females of similar body condition (Heitmeyer 1995), or reunite with the same mate in subsequent years (Robertson and Cooke 1998), they would obtain benefits that exceed the costs of attending females. If females benefit reproductively from winter pairing, then males mated to those females would also benefit. Moreover, given the consistently male-biased sex ratios of duck populations (also our population; see Fig. 1), early pairing may ensure that males get high-quality females (Spurr and Milne 1976). We do not know whether males gauge the quality or complementarity of prospective breeding partners. However, male pintails in our population seem to obtain more direct benefits from winter pairing.

Contrary to the prediction of the female-advantage hypothesis, the time budgets of feeding and frequencies of submergence in paired males were significantly higher than those in unpaired males (Table 1). Unpaired males frequently approached females while swimming. They performed courtship displays mostly toward unpaired females. However, paired males do not need to spend more time swimming to seek mates and perform courtship displays. Thus, paired males were able to spend more time feeding by saving time and energy in courtship. Many authors consider mate guarding during winter to be costly for male ducks because guarding males may spend less time feeding and more time being vigilant than nonguarding males (Rohwer and Anderson 1988). However, our results did not support this prediction. This study was conducted at only one, small sanctuary where food was provided. It is possible that supplemental food affects the behaviors of males and females. Thus, studies in multiple populations under natural habitat conditions in multiple areas and years are needed to test our conclusion that the advantage of winter pairing for males comes from having a mate *plus* having an increase in feeding frequency.

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