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Pair-bond Dissolution in Mallards

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Mallards (*Anas platyrhynchos*) form seasonally monogamous pair bonds sometime during autumn migration, on wintering areas, or during spring migration (Rohwer and Anderson 1983); nearly all pair bonds are formed by the time of spring migration (McKinney 1975). Females appear selective in choosing a mate (Weidmann and Darley 1971), likely evaluating male attributes such as age, body size, dominance rank, experience, and plumage quality (Holmberg et al. 1989, Weidmann 1990). Some of these attributes may be important in enhancing the ability of males to defend their females from unpaired males that may attempt forced copulations, and to defend areas where the female can feed undisturbed (Goodburn 1984, McKinney 1985). Thus, because paired birds tend to dominate unpaired birds and to occupy better feeding habitats (Paulus 1983 on Gadwalls [*Anas strepera*]), pair bonding appears to benefit both sexes.

However, despite the vast amount of information published on Mallards, data on pair-bond duration remain scant due to the difficulty in observing marked pairs. Although a few observations of male Mallards accompanying females with broods have been reported (Dzubin 1955, Chura 1962), visual observations of marked birds have found that many pair bonds only lasted until the onset of incubation, and nearly all terminated by the second week of incubation (Dzubin 1955, Oring 1964, Titman 1983). Studies of radio-marked Mallard pairs in Minnesota found that of 15 pairs monitored, males remained with females an average of four days into incubation (Gilmer et al. 1977). However, a study of radio-marked Mallard pairs in Iowa found that pair bonds likely were maintained into midincubation and through more than one nesting attempt (Humburg et al. 1978). Specifically, of 22 marked females whose first nesting attempts were destroyed on days 10 to 17 of incubation, 11 were identified in remating sequences of which 8 remated with their original males. Elsewhere in Iowa, among 14 radio-marked Mallard pairs, 9 females rejoined original males after first nests were destroyed (Ohde et al. 1983). There also are at least two reports of a Mallard pair bond in the wild extending beyond a single breeding season (Dwyer et al. 1973, Blohm and Mackenzie 1994). In a population of resident Mallards in urban Norway, Mjelstad and Saetersdal (1990) reported on 10 of 12 color-banded pairs that remated during the second year of the study. Mjelstad and Saetersdal argued that re-uniting of Mallard pairs may be the rule rather than the exception in sedentary urban populations.

In this paper, we present data on duration and age composition of Mallard pair bonds, and causes of pair-bond dissolution in a small sample of radio-marked Mallard pairs. In addition, we report an unusual observation of a pair of Mallards remaining together on our study area for at least three consecutive years after marking. Our data were collected in northern New York within a large wetland complex in a highly forested and agricultural region of the St. Lawrence River Valley.

From late March through late April 1990 to 1992, 388 male and 128 female Mallards were captured with decoy traps (Sharp and Lokemoen 1987) and banded with U.S. Fish and Wildlife Service aluminum bands. Individuals were aged as second-year (SY) or after-second-year (ASY) birds following criteria of Krapu

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et al. (1979), and all females were fitted with a 20-g radio transmitter (Dwyer 1972). In 1992, 16 males captured with females in the same compartment of decoy traps were fitted with radios and released along with the females. Radio-marked birds were located three to seven days per week using a hand-held yagi antenna to visually confirm pair status. Pair bonds were considered to be broken the day following the last location of the pair together. Age composition of confirmed pair bonds was compared using a G-test (PROC FREQ, SAS Institute 1988).

Nine (56%) of the 16 Mallards radioed as "pairs" were visually confirmed as paired. Pair bonds tended to consist of individuals in the same age class (G = 4.6, df = 1, P = 0.03; Table 1). All pair bonds were terminated before August, with a median date of 15 June (range 13 May-17 July). The duration of pair bonds averaged 56.1 ± SE of 7.4 days (n = 9).

Three (33%) of the nine pair bonds terminated when one member of the pair died (two males, one female), and another three (33%) ended during first nesting attempts on incubation days 9, 11, and 15. Among the remaining three pairs (33%), one female produced a nest destroyed on day 2 of incubation (pair bond was broken 44 days later), and a second female produced three nests, the first of which was destroyed on day 5 of incubation, the second on day 8 of egg laying, and the third on day 11 of incubation (pair bond was broken 10 days later). The pair bond of the third female remained intact for 71 days after capture, but the female was never located on a nest.

Another pair of Mallards captured and banded on 3 April 1990 was recaptured in the same wetland on 8 April 1991. Only the female was radioed, but each year the transmitter dropped off before radio tracking began. On 19 April 1992, we recaptured the male on the same wetland but not the female. However, during the course of several observations with a 15× to 60× spotting scope, we read the first eight of nine numbers on the female's band (viz. 1427-6404_), and the numbers matched the band numbers of the pair. Although all nine numbers had to be read in 1992 to make a positive identification, only one other female was banded in the series 1427-64040 to 64049; thus, the probability was low that the band belonged to a different female. The study ended in 1992, but in late April of 1993, a pair of banded Mallards again was observed on the same wetland (M. Henry pers. comm.). This is the only report since Dwyer et al. (1973) and Blohm and Mackenzie (1994) of a Mallard pair bond extending beyond a single breeding season, and it is the first report of a pair bond existing beyond two seasons. Our observation represented less than 1% of the 128 female Mallards captured and banded during the study. Hence, this record represents a rare event for Mallards.

In our study, pair-bond duration in Mallards was highly variable as a result of mortality and unknown factors. Providing that both members survived the breeding season, pair bonds dissolved later than generally reported in the literature. Previous studies that relied solely on visual confirmation of pair status (e.g. nasal markers) may have underestimated dates of pair-bond dissolution in Mallards (e.g. Oring 1964). We believe this discrepancy is more likely a function of the small amount of data available for Mallards, especially that resultant from telemetry work, and that maintenance of the pair bond well into incubation may be a common event for Mallards. Such a pair-bond duration likely maximizes the opportunity for the male to remain active on the breeding area and pursue extrapair copulations while his mate is least vulnerable to being fertilized (i.e. during incubation) and yet be available to remate if the female's nest is destroyed (Goodburn 1984). Theoretically, all pair bonds should be terminated once females cease renesting, because the males no longer have any opportunity to successfully inseminate females.

TABLE 1. Age composition of radio-marked Mallard pairs in northern New York during March and April 1992.[a]

	Females		
Males	ASY	SY	Total
ASY	7	3	10
SY	1	5	6
Total	8	8	16

[a] Pairs consisted predominantly of individuals of same age class (G = 4.56, df = 1, P = 0.033).

Our data support this scenario because the 1992 breeding season lasted 70 days (Losito 1993), and the average duration of pair bonds (56 days) was only 14 days shorter. Thus, mates likely were breaking up during the renesting period. Furthermore, the median date of pair-bond dissolution (15 June) was beyond the period of peak nesting (22 May) by other Mallards on our study area in 1992 (Losito 1993), suggesting that pair bonds lasted through several nesting attempts.

As the breeding season progresses and the number of unpaired males increases, paired males must defend their mates from the ever-increasing pool of unpaired or loosely paired males. These males may attempt to form pair bonds with females that have lost their mates, or to obtain extrapair copulations with paired females (Goodburn 1984, McKinney 1985). Therefore, it may benefit the female to maintain the pair bond as long as possible for protection through the breeding season and for renesting attempts. Sometime during the latter portion of the breeding season, the male's costs of maintaining the pair bond presumably outweigh the benefits, and the bond is terminated. Males initiate pair-bond dissolution by gradually decreasing the amount of time spent in the presence of their mates (Dzubin 1955, Oring 1964, Titman 1983, McKinney 1985).

Bluhm's (1985) experiments with captive Canvasbacks (*Aythya valisineria*) revealed that disrupting pair bonds caused females to forego reproduction, and the author concluded that pair bonds were critical to reproduction. There is no evidence that this happens with Mallards, as they reportedly will re-pair on the breeding grounds if necessary (Humburg et al. 1978, Ohde et al. 1983). We found that opportunities for repairing in Mallards were high, as indicated by the large proportion (33%) of pair bonds that broke up prematurely due to death of one member. Certainly, the low nest success of 18% on the study area (Losito 1993) indicates that re-pairing opportunities are frequent.

Reproductive success in Mallards is positively related to female age (Krapu and Doty 1979). The tendency for ASY females to pair with ASY males indicates that these pairs may experience better reproductive success as a result of their previous breeding experience and the experience of their partner (see Raveling 1981). However, a larger sample size, preferably with more than two age classes, would be needed to adequately test this hypothesis.

Long-term pair bonding is rarely reported in Mallards (see Dwyer et al. 1973, Blohm and Mackenzie 1994) and accounted for a meager (<1%) proportion of the pair bonds followed in this study. These isolated cases of long-term pair bonds demonstrate the behavioral plasticity exhibited in the Mallard mating system. Notwithstanding, disparate levels of breeding philopatry exhibited by male Mallards (3%; Titman 1983, Evrard 1990) compared with female Mallards (50%; Titman 1983) indicate that long-term pair ponds in Mallards indeed are rare.

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Distinctive Song of Highland Form *maculicollis* of the Red-winged Tinamou (*Rhynchotus rufescens*): Evidence for Species Rank

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The highland subspecies *maculicollis* of the Red-winged Tinamou *Rhynchotus rufescens* is known only from a small number of museum specimens. No life history data have been published. Herein I describe the highly distinctive song of this form. The song was a mysterious sound that I heard and tape recorded in several localities in the Bolivian Andes. I finally tracked down a singing bird in December 1993, near Inquisivi, departamento La Paz, Bolivia.

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Rhynchotus rufescens maculicollis occurs on grassy mountain ridges in the eastern Andes of Bolivia and northwestern Argentina at 1,000 to 3,500 m (Fjeldså and Krabbe 1990). The other subspecies of this bird are widely distributed in grassland habitats south of the Amazon, from extreme southeastern Peru to central Argentina, mostly in the lowlands but also in the highlands of eastern Brazil (Sick 1993).

A sonogram from Inquisivi and sonograms of two different birds recorded near Vallegrande, departamento Santa Cruz, are shown in Figures 1A, B, C. The song is aptly described by the local name of the bird,

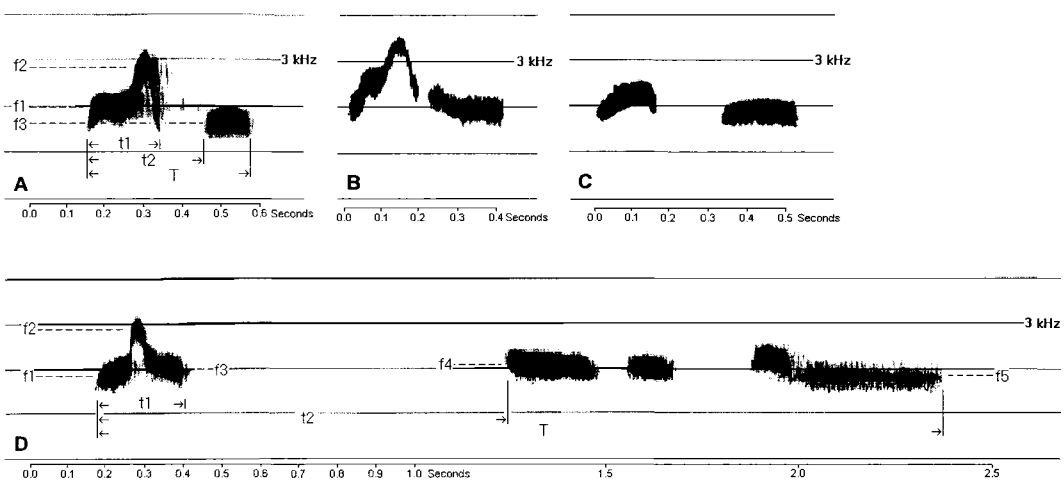

Fig. 1. Songs of *Rhynchotus* (*rufescens*) *maculicollis* (highland "race") and *R. r. rufescens* (one of three lowland races) recorded in Bolivia. Values for indicated variables are given in Tables 1 and 2. (A) *maculicollis*, Inquisivi, departamento La Paz (16°52'34"S, 67°11'42"W; 3,500 m), 12 December 1993; (B) and (C) *maculicollis*, Vallegrande, departamento Santa Cruz (18°39'30"S, 63°55'30"W; 2,400 m), 4 February 1993; (D) *r. rufescens*, Serranía de Huanchaca, departamento Santa Cruz (14°43'S, 60°30'W; 500 m), 19 April 1993.