

number of observations per ratio was increased from one to 100, the correlation coefficient between the dominance ratio and date of hatch increased from 0.52 to 0.86 (number of birds  $n = 112$  to 21). When all birds with five or more observations were included in a weighted analysis (weight = number of observations), the corresponding correlation coefficient was 0.81 ( $n = 98$ ). This figure was similar to that obtained when only ratios based on 100 observations per bird were used ( $t$ -test,  $t = 0.09$ , ns), but its confidence interval was much smaller (Fig. 1). In contrast, when significant correlations were not found between dominance ratios and other independent variables in weighted analyses (e.g., morphological characters; see Arcese and Smith 1985), neither were they found when only ratios based on a large number of observations per bird were used.

Our results suggest three conclusions about the dominance ratio: (a) the standard procedure of not weighting ratios according to their sample size and of including ratios with as few as five samples is unacceptable because of the large variance of such ratios; (b) our empirically determined weight agreed closely with the weight suggested by theory (Gilbert 1973); and (c) correlation coefficients estimated from analyses based on weighted ratios were similar to those obtained when only ratios based on a large number of observations per bird were used. However, using weighted ratios produced more accurate estimates (i.e., smaller confidence intervals) because information was retained by not excluding birds from the analyses.

Although estimates are improved by weighting, weighting is no alternative to rigorous data collection; if all ratios are based on small samples, estimation error may still

obscure important relationships. We suggest that when the structure of hierarchies is not at issue, dominance ratios can estimate dominance, and that weighting can reduce the error of these ratios.

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## PREDATION ON BLACK RAILS DURING HIGH TIDES IN SALT MARSHES<sup>1</sup>

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**Key words:** Black Rail; predation; Great Egret; Great Blue Heron; salt marsh; high tide; kleptoparasitism; Northern Harrier; Virginia Rail.

Grinnell and Miller (1944) close their account on the Black Rail (*Laterallus jamaicensis*) with the statement that the "most important hazards to existence on salt marshes appear to be extra high tides." High tides are known to destroy Black Rail nests in California salt marshes (Ingersoll 1909, Huey 1916, Dawson 1923) and during winter to cause some adults to temporarily leave marshes (Stallcup and Greenberg 1974, Manolis 1978, Winter and Manolis 1978). Our observations of predators capturing Black Rails during high tides at two California salt marshes reveal another hazard to which Grinnell and Miller (1944) may have been referring.

During the winters of 1981 to 1982 and 1982 to 1983, we coordinated 11 high tide censuses of Black Rails at Corte Madera Ecological Reserve (CMER), a 35 ha *Salicornia virginica*-dominated salt marsh on the northwest shore of San Francisco Bay, Marin County, California. Volunteer observers, stationed around the margin of the

marsh, counted the numbers of each rail species leaving the marsh, the times of departure, the modes of exodus (swimming, walking, or flying), and the types of cover into which they disappeared. Mostly this cover was sweet fennel (*Foeniculum vulgare*) which grew in thick stands adjacent to the salt marsh. In 290 observer hr spread over 11 days, we saw 31 Black Rails, 86 Clapper Rails (*Rallus longirostris*), 26 Virginia Rails (*R. limicola*), and 12 Soras (*Porzana carolina*) leaving the marsh.

No one saw rails captured in the upland cover, but Northern Harriers (*Circus cyaneus*) caught two Black Rails that remained in the marsh after inundation, when partly submerged gum plants (*Grindelia* sp.) and widely scattered tops of the tallest *Salicornia* plants were the only emergent marsh vegetation. On 29 November 1982, 30 min before high tide (1.9 m above mean low water), Evens saw a female harrier land on a *Grindelia* bush. During a 10 min observation period, it rose in the air then landed several times before finally hovering over and dropping into the bush, rising afterwards with an apparent Black Rail. About 12 Ring-billed Gulls (*Larus delawarensis*) converged on the harrier as it flew off, causing it to drop the rail in the water. One gull picked up the slow-swimming rail in its bill, then dropped it. After three attempts the harrier retrieved the rail from the water, flew off to an emergent bush, and ate the rail. On 30 December, 25 min before a similar high tide, Evens and two other observers saw a

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harrier capture another small swimming rail. When the harrier rose from a *Grindelia* bush about 2 m from the rail, the rail dove under water but was seized by the harrier as it surfaced. The hawk ate its quarry on a levee, leaving behind the head, wings, and stomach of a Black Rail.

To supplement observations at CMER, Evens (and on two occasions another observer) watched avian predators hunt during high tides at a 45 ha salt marsh at the southern end of Tomales Bay, Marin County, California, on 11 days between 21 November 1984 and 19 January 1985. Unlike CMER, the Tomales Bay marsh lacked bordering upland cover and was surrounded by open water at high tide. The observations took place up to 75 min before and 35 min after high tides, which varied from 1.7 to 2.0 m above mean low water. During 15.1 hr of observation, Great Egrets (*Casmerodius albus*) captured 15 Black Rails and Great Blue Herons (*Ardea herodias*) captured 2 Black Rails. When hunting, egrets typically walked slowly; prior to prey-capture attempts they paused, peered-over, headswayed, then used a bill-thrust to seize rails in emergent vegetation (behavioral nomenclature after Kushlan 1978, and Hancock and Kushlan 1984). On 11 occasions egrets flushed Black Rails which in 8 cases flew 20 to 30 m before dropping into emergent vegetation and escaping. However, in the three remaining cases the rails flew over open water and were overtaken; in two cases egrets captured rails in flight, but in one the rail was knocked into the water and then captured by the egret after it surfaced from a dive.

Other accounts of Black Rail mortality during high tides in California include: (1) one eaten by a Great Egret at Palo Alto Baylands, Santa Clara County, on 12 December 1981 (J. Morlan, pers. comm., LeValley and Evens 1982); (2) one eaten by a Great Blue Heron in the same location on 9 January 1982 (J. Langham, pers. comm., LeValley and Evens 1982); (3) one probable Black Rail caught and eaten by a Northern Harrier at Upper Newport Bay, San Diego County, on 2 January 1983 (Suffel 1983); (4) one probable Black Rail captured on the water by a Ring-billed Gull at CMER on 19 December 1983 (D. Sierra, pers. comm.); and (5) one found freshly dead, apparently trampled by birdwatchers, at Benecia State Park, Contra Costa County, on 10 December 1977 (Winter and Manolis 1978).

We know of only four other published accounts of predation on Black Rails in California. One involves a female caught by a domestic cat (*Felis catus*) in downtown San Francisco, San Francisco County, on 9 August 1945 (Orr 1947); another involves a bird impaled on a barbed wire fence on 25 February 1928 at Playa del Rey marsh, Los Angeles County (Ewan 1928). In the latter instance, the fact that the body was impaled suggests it was killed by a shrike (*Lanius* sp.) (Ewan 1928) or it struck the fence in flight. The remains of a Black Rail were found in the stomach of a Short-eared Owl (*Asio flammeus*) on 11 March 1925 (Huey 1926), and a Black Rail was reported killed by a Short-eared Owl on 7 February 1932 between China Camp and Santa Venetia, Marin County (Stephens and Pringle 1933). These four accounts do not provide, however, sufficient information to determine any relationship between mortality and tidal influence.

We also witnessed predation attempts on other species of rails at CMER and Tomales Bay during the observation periods. At CMER we saw unsuccessful attempts by harriers on Sora, Virginia Rails, and Clapper Rails. At Tomales Bay, Great Egrets captured 2 Virginia Rails and 1 unidentified rail, Great Blue Herons captured 5 Virginia Rails and 4 unidentified rails, and harriers captured 1 Virginia Rail. Two of these captures also involved kleptoparasitic interactions, with a heron stealing a Virginia Rail from an egret and an egret stealing a Virginia Rail from another egret.

The observations summarized above suggest avian predators may be responsible for a significant amount of Black Rail mortality, and that herons and egrets eat rails more commonly than the scattered references on this topic indicate (references cited above, Murphy 1976, Campbell and Wolf 1977, Hewson and Hancox 1979). Our observations showed predation occurring during high tides when flooded marshes provided minimal vegetative cover. Murphy (1976) describes a similar situation for Grey Herons (*Ardea cinerea*) preying on Water Rails (*R. aquaticus*) in Britain. We lack comparative data to evaluate avian predator success in capturing rails at other tides but suspect it is much lower, since in the course of hundreds of hours of field work in salt marshes at other tides we have never seen predators catch rails. A study comparing rates of predation on rails at different tides would be useful to corroborate our suspicion that tides play a role in increasing the susceptibility of rails to predators. In such a study it would also be interesting to determine if avian, and possibly mammalian, predators used high tides as a cue for increased foraging effort in tidal marshes.

Vegetation peripheral to marshes may partially offset predation risk by providing rails with alternate cover at high tides. Rails in upland habitat adjacent to the marsh at CMER during high tides were taken less often by avian predators than were those at Tomales Bay, where cover peripheral to the marsh was lacking. However, conclusive evidence for the importance of peripheral uplands to rails requires more detailed studies that consider not only vegetative cover but also the size of predator and prey populations.

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## PARENTAL CARE AT A RED-TAILED HAWK NEST TENDED BY THREE ADULTS<sup>1</sup>

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**Key words:** *Red-tailed Hawk*; *Buteo jamaicensis*; breeding biology; helpers; brooding behavior.

Although the presence of more than two adults simultaneously tending the same nest has been reported for several species of raptors (Newton 1979), quantitative descriptions of nest attendance in these instances are scant. Wiley (1975) reported the first case of three adult Red-tailed Hawks (*Buteo jamaicensis*) tending a nest. We report a second case of three adults at a Red-tailed Hawk nest, and we compare nest attendance patterns at this nest with those at a nest tended by two adults.

Two Red-tailed Hawk nests, one tended by three adults (Nest 1) and the other by two adults (Nest 2) were studied in Dane County, Wisconsin. Both nests were on white oaks (*Quercus alba*) approximately 14 m from the ground and had similar canopy cover. The nests were located on adjacent territories in small (1.0-ha) woodlots surrounded by pastures. Inter-nest distance was 0.9 km. Habitat composition and human activity surrounding the nests were similar.

We first visited the nests on 19 May 1984. Nestlings were aged by measuring the length of the fourth primary (Petersen and Thompson 1977). Nest 1 had one three-week-old young and was defended by three adults, whereas Nest 2 had two two-week-old young and was defended by two adults. During each of four subsequent visits to Nest 1 (20, 23, 27, and 29 May), three adults simultaneously defended the nest by calling and flying to within 50 m of the person at the nest. During a visit to Nest 1 on the evening of 20 May, we saw one adult roosting at the nest while the other two roosted within 30 m of the nest.

The trio consisted of one male (distinguished by his smaller size and aerial displays) and two females. Female A had a complete set of primaries whereas Female B was missing primary No. 6 from the right wing. These differences allowed us to recognize each individual in flight. On 27 May all three birds attending Nest 1 soared together above the nest for over one hour. With prey in his talons,

the male approached both females and performed undulating flight displays. We never observed overt aggressive interactions among the three birds. We did not observe the trio during pre-laying or incubation periods when copulations occurred; therefore we did not know the original clutch size at the nest and whether the extra female was a nonreproductive "helper" or a second mate in a polygynous bond.

On 29 May we removed one nestling from Nest 2 and exchanged it for the nestling at Nest 1. The nestling from Nest 1 was fostered into a third Red-tailed Hawk nest that had originally contained only one young. These exchanges resulted in Nest 1 and Nest 2 each having a single young of comparable age. On the day of the exchange we also placed an automatic time-lapse camera at each nest. We allowed three days for the birds to adjust to their new brood size, and we then monitored each nest for a minimum of 12 hr each day, between 0530 and 2100 on 1, 2, 5, and 6 June. Photographs were taken at 30-sec intervals. Observations ended on 7 June when we removed the cameras.

Differences in size and age of broods and in habitat variables, weather, and temporal factors can obscure comparisons of the effect of helping behavior at different nests (Brown 1978, Rabenold 1984). Habitat, weather, and temporal factors were similar between the two nests in this study due to their location, geographic proximity, and our concurrent monitoring. Our brood manipulation controlled for size and age of broods. Presumably, nest attendance patterns were mostly influenced by the number of adults tending the nest and by individual differences among these adults.

We inspected 11,811 photographs taken during four days of time-lapse photography at both nests, tallied the number of photographs in which adults were at the nests, and recorded whether they were feeding or brooding. From these photographs we then calculated the amount of time spent at the nest and the amount spent brooding. We could distinguish between the two females at Nest 1 by differences in throat coloration, but for almost 40% of the visits we were unable to identify the individual at the nest. Identification of prey items could not be made from the photographs.

Both females at Nest 1 defended the nest and fed, brooded, and preened the nestling. When defending, Female A consistently called more often and approached closer (10 m) to the person at the nest than did Female B (30 to 40 m). The male called less frequently and did not approach us as closely (>40 m) as either female. During one visit

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