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ALARM CALLS, HABITUATION AND FALCON PREDATION ON SHOREBIRDS

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INTRODUCTION

The ability to recognize predators and avoid predation are critical elements in the life history strategy of most birds. Habituation to improper stimuli and anti-habituation to predators are thought to be innate discriminatory mechanisms (Mueller & Parker 1980) which develop as an animal experiences a variety of contexts (Shalter 1984, Seyfarth & Cheney 1986). The ability to minimize habituation to predators, especially predators which are hunting, is perhaps more important than habituation to improper stimuli. Habituation to improper stimuli appears to develop in concert with anti-habituation to appropriate sources (*e.g.* Seyfarth & Cheney 1986). Anti-habituation must develop quickly because "...the inability to keep reacting (or at least keeping vigilant) to a predator, unless it is likely to attack, would make life very short" (Shalter 1984).

One way in which birds avoid predation is through the use of auditory signals. These signals advertise knowledge of a predator's presence and may be intended for the predator itself or as a warning to others. Habituation and alarm signals are intimately linked; the accurate assessment of predation risk is prerequisite to effective alarm signaling. In turn, selective advantage is accrued only by those who properly interpret signals (but see Charnov & Krebs 1975).

In this paper I discuss habituation and alarm signaling as these relate to real or potential predatory contexts experienced by shorebirds wintering in western Washington. In addition, I speculate about possible adaptive functions of these behaviour types, some of which may apply to shorebirds susceptible to similar predation pressures in other wintering areas. Specifically, I speculate about 1) a possible relationship between sandpiper alarm calls and observed regional differences in predator efficiency, 2) the relationship between sandpipers and shorebirds which give mobbing alarm calls, and 3) the significance of habituation exhibited by larger shorebirds during hunting flights by falcons.

BACKGROUND ON ALARM CALLS

Birds, like mammals, compare incoming signals using binaural phase and intensity cues to locate sounds (Marler 1955, 1957). Binaural comparison of low frequency signals reveals differences in phase (time difference) while high frequency signals are interpreted through differences in intensity (see Gourevitch 1978, Knudsen 1980). Effective binaural comparison of phase and intensity differences are made within largely independent frequency ranges. Between these frequency ranges sounds are localized less effectively (see Calford *et al.* 1985 for discussion of frequency gaps in raptors). In humans this crossover range occurs at *c.* 1.5-3 kHz and in birds and mammals it is higher, depending on the overall auditory range (in kHz) and head size (distance between ears for binaural comparison).

Calls given by birds in response to predators are generally of two varieties: mobbing calls and "seeet" alarm calls (Marler 1955). Perception advertisement appears to be an important benefit of mobbing calls. The perception advertisement hypothesis states that an obvious display by the potential prey will advertise to a predator that it has been seen, thus reducing the probability of attack (for review see Klump & Shalter 1984). In contrast, "seeet" calls are thought to be difficult to locate (Marler 1955, Brown 1982, but see Shalter 1978), therefore allowing signalers to alert others in the group while incurring little risk themselves.

SANDPIPER ALARM CALLS

Of particular interest to this discussion are the alarm calls of the Dunlin *Calidris alpina*, Western Sandpiper *C. mauri*, and Least Sandpiper *C. minutilla*. The alarm call frequency for *C. mauri* has not been published but the alarm call frequency for *C. alpina, C. minutilla* and, for comparison, two other Holarctic shorebirds (Little Stint *C. minuta* and Temminck's Stint *C. temminckii*) are presented in Table 1. The alarm call of Little Stint occurs at 3.5-5.3 kHz and the alarm call of Temminck's Stint occurs in the frequency range 3-5.8 kHz; all others occur in the range 2.0-4.9 kHz. It is not known whether any of the calls are difficult for falcon predators to localize. Although Klump *et al.* (1986) suggested that hearing of Sparrowhawks *Accipter nisus* should be best in the 3-5 kHz range, other studies (Coles *et al.* 1980, Calford *et al.* 1985) have documented frequency gaps where directionality is ineffectual (see also Brown 1982). Consequently, some sandpiper calls may be difficult for certain falcon species to localize.

If the alarm calls of *C. mauri* or *C. minutilla* (and other sandpipers) species are non-localizable, other species in winter flocks containing these species might benefit if 1) these sandpipers regularly issue the call knowing that it places them at no greater risk (see Sherman 1985), 2) other flock members properly interpret the alarm signal, and 3) the signal provides an early warning (or other information) of impending danger. Signalers may benefit from association with a flock, for example if the probability of predation decreases with increasing flock size (Kus 1985).

Leger & Nelson (1982) found that Dunlins and Western Sandpipers foraging on tidal flats near saltmarsh had a much more pronounced response to playbacks of interspecific alarm calls than birds further away from the saltmarsh, regardless of the position of playback speakers. They also found that sandpipers closest to saltmarsh were first to react to human disturbance. Given the relative spatial foraging patterns of these two species (the Dunlin forages near water's edge while the Western Sandpiper forages on tidal flats away from the water), Western Sandpipers would probably be first to detect attacks originating from the cover of adjacent saltmarsh. This suggests that non-localizable (or other) calls given by prey species perform an important function in this context.

Table 1. Approximate frequency range (in kHz) of alarm calls of some Holarctic *Calidris* sandpipers.[a]

Species	Approximate frequency range
Dunlin *C. alpina*	2.0-3.8
Least Sandpiper *C. minutilla*	2.0-4.9
Little Stint *C. minuta*	3.5-5.3
Temminck's Stint *C. temminckii*	3.0-5.8

[a] From Cramp & Simmons (1983).

If alarm calls effectively warn members of a mixed-species flock, mixed-species flocks of shorebirds should be more efficient at avoiding predation. Page & Whitacre (1975) found that success rates for Merlins hunting a mixed-species flocks of sandpipers in California was low (12.8%). In contrast, the success rate for Merlins hunting Dunlins in Washington is significantly higher (22.5%; Buchanan *et al.* 1988). Western and Least Sandpipers are much more common during winter in California than in Washington, where the shorebird community is less diverse (Pitelka 1979). This circumstantial evidence is consistent with the hypothesis that certain sandpiper alarm calls effectively announce attack by falcon predators. Other factors, however, may also influence the observed differences in hunting success rates (see below).

The hunting behaviour exhibited by Merlins which hunt shorebirds is unexpected for a predator presumably reacting to the development of adaptive behaviour by its prey (*e.g.* an escalation of the "arms race"; see Dawkins & Krebs 1979). For example, if sandpipers which give effective alarm calls are common in mixed flocks, one might expect Merlins to use a more varied repertoire of hunting technique, assuming that stealth flights are effectively announced by an alarm call and that other hunting methods pose no constraints. Studies in California, however, have shown that Merlins typically use low stealth flights when hunting, and experience a relatively low success rate for hunting flights (Page & Whitacre 1975, Kus 1985). On the other hand, in Washington, where the Western Sandpiper is uncommon and the Least Sandpiper is generally absent, Merlins might be expected to use stealth attacks more often, assuming that Dunlin flocks without a certain proportion of other sandpipers are somehow less responsive to stealth attacks. Low stealth flights are, however, less common than stoops in Washington (Buchanan *et al.* 1988).

If qualitative interspecific differences in alarm calls are lacking or sandpiper alarm calls are, in fact, localizable then perhaps the differences in hunting behaviour and performance noted above are related to region-specific factors. For instance, perhaps low stealth flights by Merlins in California predominate because they are less likely to be observed by larger shorebirds such as Willets *Catoptrophorus semipalmatus* and Marbled Godwit *Limosa fedoa*. These species might, because of their size, be more effective at detecting the approach of predators (but see below and Metcalfe 1984). High flights by Merlins in Washington may allow a Merlin to continuously assess its chances of being kleptoparasitized after capturing prey (Buchanan 1988). There is clearly room for research on this topic.

OTHER ALARM CALLS

The Black-bellied Plover *Pluvialis squatarola* appears to use identical calls for alarm (mobbing) and group purposes (pers. obs.) (see Owens & Goss-Custard 1976). As signalers, the relationship between this species and Dunlins or other sandpipers which might receive the signal, is unclear. Grey Plovers and Dunlins often forage in close proximity in western Washington. When attacked by a Merlin, a flock of *C. alpina* in western Washington will coalesce into a tight formation and engage in predator evasion flight above open water or tidal flats (Buchanan *et al.* 1988). Grey Plovers also respond by making predator evasion flights (pers. obs.). Dunlins appear to rely on the plover's alarm (mobbing) call as a warning signal. This is similar to the relationship between Dunlins and Golden Plovers *P. apricaria* at European nesting areas (Byrkjeda & Kalas 1983, Thompson & Thompson 1985). Those studies found that Dunlins benefitted by using the early-warning capabilities of Golden Plovers to reduce their predation risk. Because food overlap between Golden Plovers and Dunlins was high, the food supply to Golden Plovers was decreased as a result of their greater vigilance (Byrkjeda & Kalas 1983). Thompson & Thompson (1985) thought that greater responsiveness in mixed flocks was a residual adaptation (or "Exaptation") (see Gould & Vrba 1982) because Golden Plovers and Dunlins may at one time have nested colonially (Hale 1980).

During winter, association with Grey Plovers may benefit Dunlins if the early warning capabilities of Grey Plovers more effectively facilitate flock formation. This could arise because in some regions Dunlins in flight may have a lower probability of being preyed upon (see Page & Whitacre 1975). However, it can also be reasoned that Grey Plovers will benefit most by giving the mobbing call if this diverts attention away. According to the prey manipulation theory (Charnov & Krebs 1975), a caller uses an alarm call to manipulate the behaviour of conspecifics, thereby diverting attention away from itself. Although the probability of a Merlin attacking a Grey Plover appears low, Grey Plovers are not habituated to this predator. Perhaps the response occurs before they can differentiate between Merlins and the larger Peregrine Falcons, a predator easily capable of capturing Grey Plovers (see below) and the call is given to divert attention away. This suggests that a variant of the prey manipulation theory cannot be discounted without further research.

HABITUATION

Grey Plovers and Dunlins respond similarly to the presence of Merlins. A Merlin detected flying within the range of human vision will elicit predator evasion behaviour. Both species will, however, quickly habituate to a Merlin perched in the open (pers. obs.; and see Bildstein 1982). Although successful attacks are occasionally launched from such perches within a 75m of foraging or roosting Dunlin flocks (pers. obs.), the ability to habituate to a nearby predator mat partially counteract the risk by allowing more time to forage.

As stated above, Grey Plovers may be unable to differentiate immediately between rapidly flying Merlins and Peregrines. This may be exaptative behaviour, since I have not seen Merlins attack this species and Peregrines were absent from most sites where I have observed Grey Plovers. It is possible that the Peregrine was a more important predator to Grey Plovers (and Dunlins) as recently as 40 years ago (*c.* 1945) prior to the drastic population decline of this species (Hickey 1969). Even so, it is highly adaptive to react in the predator context, even if recognition is not certain. Habituation to a capable predator could prove fatal (see Hirsch & Bolles 1980).

Boyce (1985) found that three large shorebird species in northern California (American Avocet *Recurvirostra americana*, Willet and Marbled Godwit) were habituated to Merlins and exhibited predator evasion behaviour only when Peregrines or Prairie Falcons *F. mexicanus* hunted in the area, indicating that some species differentiate between similar predators and respond to those which represent a real threat (see Seyfarth & Cheney 1986). This suggests that habituation to Merlins may be more effective in areas where Peregrines or other predators are also present.

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REVIEWS AND ABSTRACTS

KONDRATIEV,A.Y. (Ed.) (1988) Bulletin of the Working Group on Waders. (Russian.) Pp. 46. Vladivostock: All-Union Ornithological Society (USSR Academy of Sciences) and Institute for the Study of Biological Problems of the North (Far East Branch of the USSR Academy of Sciences). 0.15 roubles. 300 copies printed.

The 3rd All-Union Wader Study Conference held in Moscow in October 1987 noted that progress had been made in various aspects of wader research in recent years but strongly felt that Soviet ornithology was progressively falling behind other countries in such projects as mapping main migration stopover sites and accumulating census data to assess their potential as wetlands of national or international importance. Man-made changes to wader habitats required more thorough quantitative investigation, as did the effects of shooting and collecting on wader populations.

With the aim of achieving more effective planning and co-ordination in these and many other tasks, the Soviet Working Group on Waders was set up at the 1987 Conference. All 74 delegates at the Conference were automatically elected members and others will doubtless be encouraged to come forward from the ranks of the still youthful (founded in the early 1980s) USSR Ornithological Society. The Rules of the new Working Group are set out on pp. 5-7 of this first Bulletin which is designed to be the main publication, appearing annually. The Group's 'Bureau' (Executive Committee) consists of V.E. Flint (Consultant), P.S. Tomkovich (Chairman), A.Ya. Kondratiev (Vice-Chairman and Co-ordinator for studies of wader bioenergetics), T.R. Andreeva (Secretary and Co-ordinator for food and feeding studies of arctic and subarctic waders, M.E. Zhmud (Co-ordinator for the Ukraine and Eastern Black Sea region, also for population ecology), V.V. Morozov (responsible for the Group's publications and for informing the Wader Study Group about current Soviet literature on waders), V.V. Khrokov (Co-ordinator for Kazakhstan and Central Asia), A.K. Yurlov (Co-ordinator for study of the critically endangered Slender-billed Curlew *Numenius tenuirostris* in West Siberia). A further circle of co-ordinators includes I.I. Byshnev (Baltic Region and Belorussia), V.S. Sarychev (Central European part of the USSR), I.I. Chernichko (Programme for the study of Dunlin *Calidris alpina* movements), A.A. Vinokurov and E.I. Gavrilov (ringing and marking programme) and G.N. Molodan (Black-winged Stilt *Himantopus himantopus* study programme).

More volunteers are needed to take responsibility for various regions and study topics. It was considered essential to undertake a country-wide study programme and the Group proposed to focus on the widespread and familiar Lapwing *Vanellus vanellus.* The Executive Committee hopes to improve identification skills by building up a collection of photographs and skins; it will also assess records and journal editors are encouraged not to publish unusual wader records before they have been accepted by the Committee. There are to be more (following one at the 3rd Wader Conference) photographic exhibitions and competitions and nominations are invited for the best wader paper or book of 1988.

Before the next (4th) Soviet Wader Study Conference meets in Donetsk in 1990, it is clearly hoped that a start will have been made on better co-ordinated and more vigorous