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ECOLOGICAL AND EVOLUTIONARY PERSPECTIVES ON ESCAPE FROM PREDATORY ATTACK: A SURVEY OF NORTH AMERICAN BIRDS

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ABSTRACT.—Growing evidence suggests that an understanding of avian anti-predatory escape tactics is important in understanding the way in which predators influence avian ecological systems. Of key importance appears to be the way in which a bird's perception of predation risk reflects an interaction between its tactic of escape from attacks and the physical structure of its environment: a given habitat may be avoided as too risky if a bird's escape tactic does not match the physical structure (e.g., vegetational characteristics, aspects of local topography) of that habitat. However, escape tactics in North American birds are poorly characterized. Thus, this survey brings together many observations of predator-prey encounters scattered over a century's worth of ornithological literature in an effort to identify both the major tactics of escape from predatory attack and their respective ecological implications. Various escape tactics also appear to be consistently associated with certain life-history traits, and these associations are explored from both taxonomic and phylogenetic perspectives. The current state of knowledge regarding escape tactics is hindered by incomplete taxonomic coverage of the available observations and various biases in the reporting thereof. Nonetheless, this survey provides further insight into the way in which predators may influence avian ecological systems, even when actual predation in such systems is numerically insignificant. *Received 27 March 1992, accepted 1 Oct. 1992.*

Evolutionary ecologists have not viewed predation as a major force in avian ecological systems (Wiens 1989). Some recent studies on nest predation (and brood parasitism) in fragmented forests may change this view (Brittingham and Temple 1983, Wilcove 1985, Martin 1988, Robinson 1992; see also Wiens 1989), but few would consider predation on adult

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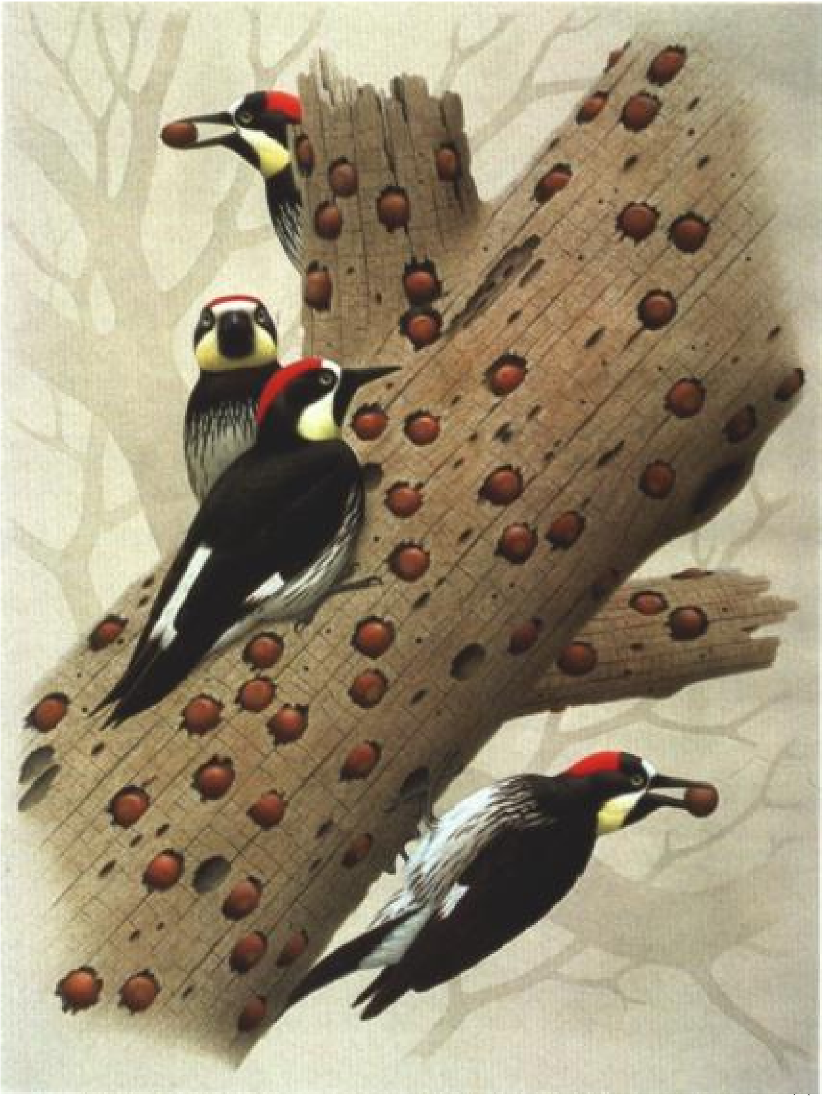
Acorn Woodpecker (*Melanerpes formicivorus*). Original painting by William Zimmerman from "Life histories of North American woodpeckers," Indiana University Press, Bloomington, Indiana, 1992 (Copyright 1992 by William Zimmerman).



birds to be important in ecological systems (but see Page and Whitacre 1975, Perrins and Geer 1980, Marcström et al. 1988). This situation contrasts markedly with that in aquatic ecology, in which predation on all life stages of a host of creatures is of obvious importance (Zaret 1980, Kerfoot and Sih 1987). Predators may also be important in the regulation of mammalian ecological systems (e.g., Desy and Batzli 1989, Hanski et al. 1991). Predators may indeed have very different effects in avian vs other systems, but such a perception may reflect merely a difference in historical emphases in these ecological subdisciplines, with avian ecology most strongly influenced by the competition paradigm (Wiens 1989).

For present purposes, I accept the view that predation on adult birds (i.e., removal of adults) is ecologically insignificant. However, it is important to distinguish between the influence of predators vs predation: insignificant predation does not rule-out a major role for predators in avian systems. Much recent work in behavioral ecology (Lima and Dill 1990) suggests that the mere presence of predators in a system elicits antipredator behavior that renders prey difficult to capture. Far from rendering predators impotent, effective anti-predatory behavior provides an avenue through which predators may exert strong effects on avian systems.

My emphasis regarding avian predator-prey interactions is the way in which a bird's escape tactic influences its perception of the risk of predation. A key aspect of such perceptions is the way in which the physical structure of the environment influences escape from predatory attack. Virtually all escape tactics described below depend upon some aspect of a bird's physical environment; this might be the presence and depth of water or snow, the topography of the local terrain, a clear path for flight, or the presence of dense vegetation. A largely unexplored consequence of such dependencies is the possibility that the nature of these physical structures is critical in determining the ecological distribution of a given species. Put differently, birds are unlikely to settle in a habitat in which they perceive a low probability of escape and thus a high risk of predation (Lima and Dill 1990). Overall, I believe that this "escape" perspective offers much insight into the influence of predators on avian ecological systems, much as it has in certain mammalian systems (Rosenzweig 1973, Kotler and Brown 1988, Brown 1988, Kotler et al. 1991, Longland and Price 1991).

SCOPE, METHODS, AND DEFINITIONS

There are many ways to avoid death in an encounter with a predator (Lima and Dill 1990). For instance, a bird may "freeze" and thus avoid detection (e.g., Morse 1970), or, if detected, prevent actual attack by a quick retreat to some refuge. Perhaps the most critical point in this interaction occurs when a bird (or flock) is actually attacked and pursued by a predator; the behavior of such birds is my focus in this survey of escape tactics.

Observations of predatory attacks on birds are made infrequently. This is true despite the fact, for instance, that an individual Cooper's Hawk (*Accipiter cooperii*) might capture hundreds of birds per year. However, the scarcity of such observations has prompted many biologists to report them in the scientific literature. These published observations form the basis of this paper, and were obtained from a survey of the major North American ornithological journals (The Auk, Condor, The Journal of Field Ornithology, The Wilson Bulletin) and many regional ornithological journals in relatively wide circulation (e.g., Western Birds). The entire publication series of each journal was examined issue-by-issue, via the table of contents, for papers that might contain information on predator-prey encounters. Various ornithological monographs (e.g., Bent series) and journals of natural history (e.g., Great Basin Naturalist, Southwestern Naturalist, Canadian Field-Naturalist) were similarly surveyed, as was the ecological and behavioral literature on predator-prey interactions. I also sought the observations of several colleagues particularly familiar with the natural history of taxa for which I could locate virtually no published information. The following survey thus comprises these many observations, together with my personal observations on predatory attacks made during several behavioral studies. Overall, I was able to obtain some information on about 60% of the families and 23% of the species of birds breeding in North America. Note that observations of "escape" in response to humans are not generally included in this survey, as such responses may not be indicative of escape from true predators. Furthermore, a few observations from outside North America are included for some cosmopolitan species.

Observations differ greatly in the behavioral detail that they provide. Observations included in this survey provided information on the type of predator involved, the "escape destination" of the prey (e.g., dense vegetation), and preferably some information on the prey's behavior during the pursuit. This information is conveyed in a three-part code. The first part describes the place where the prey was attacked (e.g., in the air) and its escape destination (e.g., water). The second part indicates the identity of the predator involved, and the third indicates behavior observed during escape (if available). The resulting code is interpreted as follows. For example, given the symbols in Appendix I, the code "A → W|F|pl" indicates that the bird in question was attacked by a falcon (F) while flying in the air (A), and that its escape destination was a body of water (W). Furthermore, the bird plunged into the water at high speed (pl). Note that multiple observations involving the same escape destination and general prey behavior are combined into a single code when possible. All behavioral interactions took place in flight unless indicated otherwise.

Some potential biases and other problems are unavoidable in these observations. For instance, literature reports may be biased towards the more "spectacular" predators (e.g., the larger falcons) and, perhaps also, the more spectacular instances of attack and escape. Thus the full range of predators experienced by a given species, or the full range of its behavioral escape repertoire, may not be adequately represented. In addition, there is often little behavioral information in a given observation beyond that needed to determine the "place" data in the first part of the escape code. Thus the last part of the code is often blank, and the overall description of escape is therefore limited. Finally, there are marked taxonomic and seasonal biases in the available observations. Taxonomically, the coverage in some groups is very good, while data are completely lacking in others. Taxa comprising the larger birds also have poor coverage, perhaps reflecting a lack of many serious predators on such birds. Seasonally, observations are limited to non-breeding (wintering) birds, with very few exceptions as noted. The reason for this seasonal bias is obscure. As a result, however, neotropical migrants are poorly characterized in terms of escape behavior.

ESCAPE TACTICS: A TAXONOMIC SURVEY

The survey (Appendix I) is organized taxonomically as per the AOU (1983) checklist and supplements. More than one "interaction code" for a given species in Appendix I indicates some flexibility in escape behavior; the first indicates the apparently preferred (and presumably the most effective) escape tactic. Scientific names of species may be found in Appendix I, if not given within the paper.

Gaviiformes through Pelecaniformes.—Readily apparent from Appendix I is the lack of observations for the nine families comprising the first four orders. A common thread linking these birds is their relatively large size and, for many, a marine/pelagic lifestyle. Thus, they may collectively have relatively few predators. However, the smaller procellariiforms (Hydrobatidae) may suffer significant predation (Watanuki 1986, Paine et al. 1990). In fact, observations of Peregrine Falcons (*Falco peregrinus*) hunting far at sea (Voous 1961, Rogers and Leatherwood 1981) and closer to shore (Walker 1988) indicate that storm-petrels are relatively easy prey. In any case, it seems likely that many of these birds would attempt to dive into water to escape attack (as did an unidentified small grebe, Appendix I).

Ciconiiformes.—Several observations exist for the herons and allies which may, despite their relatively large size, suffer considerable predation (Hunt et al. 1975, Caldwell 1986). The largest of these birds, Great Blue Herons and spoonbills, may escape attack by a simple threat display. Smaller herons typical of exposed coastal situations seem to use an aerial escape tactic, at least in response to attack by *Buteo* hawks. Herons typical of vegetated habitats (e.g., Green-backed Herons) may use vegetation as a refuge from attack.

Anseriformes.—Water is a common and apparently preferred escape destination for many ducks (Anatidae) under attack from large falcons (Dekker 1987). Ducks feeding on the water's surface simply dive to escape attack, while those attacked in the air often dive directly into water. I suspect that the smaller ducks (e.g., Green-winged Teal) may also engage in a socially-coordinated aerial escape tactic (as do most shorebirds, see below) based on their coordinated movement during casual flight, but I cannot find any explicit observations of this (but see Driver and Humphries 1988). Many freshwater ducks will also plunge into herbaceous vegetation when hard pressed or too far away from water (D. Dekker 1987, pers. comm.). This potentially injurious escape tactic is performed at high speed and seems to be a last-ditch attempt to avoid capture. The few available observations for marine ducks indicate water-based escape tactics, but note the aerial tactic used by a Common Elder in response to attack by a seal.

The larger members of this order (swans and geese) are largely absent from Appendix I. However, Bregnballe and Madsen (1990) report that molting (non-flying) Brent Geese (*Branta bernicla hrota*) in Svalbard, when attacked by skuas and foxes, ran inland to hide in a cliff, whereas Barnacle Geese (*B. leucopsis*) ran to the sea. The basis for this difference in behavior is not clear.

Falconiformes.—The lack of observations of escape in raptors is understandable, but several instances of large raptors killing smaller ones have been reported (Klem et al. 1985). Escape behavior has been observed in the smaller falcons (Appendix I), whose aerial escape tactic involves speed and relative maneuverability.

Galliformes.—Escape to woody vegetation is a common tactic among the galliforms (quail, grouse, etc.). There is also an indication that the larger, presumably faster (Peters 1983) grouse use an "aerial" tactic in which they simply out-distance raptors, at least when attacked by the slower ones. Ruffed Grouse may use such an aerial tactic in a woodland setting but nonetheless fly very close to vegetation in an apparent effort to thwart a pursuing predator (pers. obs.). Ptarmigans exhibit both a vegetation-based tactic and a gravity-assisted, speed-based aerial tactic involving downslope flight in steep terrain. Such a terrain-based aerial tactic reaches its zenith in the Himalayan Snowcock, which have been introduced in Nevada. When attacked by Golden Eagles (*Aquila chrysaetos*), these large birds run down-slope, launch into the air, set their wings, and dive down steep slopes and over cliffs (Bland and Temple 1990).

Gruiformes.—Rails (Rallidae) exhibit a vegetation-based escape tactic which involves disappearing into thick herbaceous vegetation. Also indicated is a water-based (diving) tactic (Appendix I). This diving tactic is also apparent in the more aquatic members of this family (coots, moorhens, etc.). No information is available on the other two families in this order (Appendix I); the cranes (Gruidae) in particular may be too large for most predators.

Charadriiformes.—Observations on escape behavior in this order are limited primarily to the Scolopacidae (sandpipers). In fact, studies of escape in the Dunlin (Davis 1980, Potts 1984, Buchanan et al. 1988) are notable for their breadth and detail. Dunlins use the "classic," socially coordinated aerial escape tactic, in which individual birds in a compact flock coordinate their flight movements to such an extent that the entire flock appears to pulsate and maneuver as one; this is the "united, erratic display" of Driver and Humphries (1988). This tactic has been observed in many of the sandpipers (Appendix I). However, it is not clear whether the escape tactic of larger sandpipers is so strongly socially coordinated.

Furthermore, night-feeding sandpipers may be reluctant to engage in aerial escape (Mouritsen 1992).

Solitary shorebirds (or those separated from their flocks), when attacked by raptors, may (i) try to out-climb the predator (e.g., Black Turnstone, Dunlin, Short-billed Dowitcher), (ii) plunge into the water and then quickly re-emerge and fly in the opposite direction (see also Morris 1990), or (iii) plunge into vegetation and attempt to hide (Pectoral Sandpiper). The extent to which various species use these tactics is not clear. Note, however, that the characteristically solitary Spotted Sandpiper appears to use only a water-based diving/submersion tactic. Interestingly, chicks in the Recurvirostridae may also dive into water when attacked (Sordahl 1982).

I was surprisingly unable to locate any acceptable information on the escape tactics of plovers (Charadriidae). I suspect, however, that escape behavior within this group is similar to that in the sandpipers for both solitary and social birds.

Only a few of the gulls and none of the terns (*Sterna* spp.) are represented in Appendix I (Laridae). These birds may not be commonly considered prey for raptors, but large falcons and eagles may regularly take gulls as prey (Murie 1940, Kruuk 1964). Available observations suggest that all gulls use an aerial escape tactic. The smaller gulls (Franklin's, Bonaparte's) appear to employ a socially coordinated tactic similar to that in shorebirds (Kruuk 1964), while larger gulls appear simply to dodge capture repeatedly just before impact until the predator gives-up the chase. These larger gulls are undoubtedly aided by their size alone.

The Alcidae are another poorly characterized group. Perhaps this reflects a relative lack of predators in their pelagic (non-breeding) habitat. Thus, it may be no surprise that the near-shore-feeding Pigeon Guillemot is one of the few species represented in Appendix I. These birds simply dive underwater to escape attack, and it appears likely that all of these sub-surface feeding birds would do the same. Note the "aerial" escape tactic of Cassin's Auklet in response to attack by a large flounder. Alcids undoubtedly suffer a relatively high risk of predation during the breeding season, when they are exposed to a large number of land-based predators (De Gange and Nelson 1982). In response to predatory Glaucous Gulls breeding Dovekies use a group-based aerial escape tactic that may involve some sort of social coordination. If alone or isolated from the group, a dovekie uses a downslope, gravity-assisted aerial escape tactic, similar to that of ptarmigans and snowcocks, that has as its destination either rock crevices or water. How common these tactics may be in breeding alcids is unknown.

Columbiformes.—The doves apparently use an aerial escape tactic involving primarily speed and aerial dodging (in the case of closely pursuing raptors). Rock Doves may use a socially-coordinated aerial escape tactic

(Driver and Humphries 1988), but the degree of coordination seems lower than in shorebirds (Pomeroy and Heppner 1992). Rock Doves may also seek a physical refuge when alone and hard-pressed by a predator; Sutton (1929) reported an instance of Rock Doves flying under powerlines to prevent capture by a diving falcon. I have also witnessed a Mourning Dove, ambushed by a Cooper's Hawk, dive full-speed into the ground (breast-first) and quickly resume flight in the opposite direction before the hawk had a chance to respond and resume chase.

Cuculiformes.—I have found no acceptable information on this group. However, it seems likely that they would seek vegetation of some sort if attacked.

Strigiformes.—The smaller owls undoubtedly fall prey to larger raptors, but I have only one observation of escape in this order, involving an incident between a Peregrine Falcon and a Short-eared Owl. The owl simply dodged attack at the last moment before impact. This may be an example of "play" in which a potentially inexperienced falcon was attempting to capture inappropriately large prey (Verbeek 1985).

Caprimulgiformes.—I have not located any acceptable references to escape in these birds. In fact, information on predation in general seems very sparse for this group.

Apodiformes.—Swifts (Apodidae) are among the most aerial of birds. Thus, it is no surprise that White-throated Swifts use an aerial escape tactic (Appendix I). Other swifts probably employ the same strategy. It may seem that such fast-flying creatures would have few predators, but in fact swifts have often been reported in diets of Peregrine Falcons (Bird and Aubry 1982).

Hummingbirds (Trochilidae) may suffer predation from opportunistic predators (Miller and Gass 1985) but little is recorded of their escape behavior. I have witnessed a Curved-billed Thrasher attack a feeding Costa's Hummingbird, which the latter deftly avoided with an aerial dodge. This may be the main escape tactic in hummingbirds.

Coraciiformes.—The Belted Kingfisher (Alcedinidae) essentially uses its feeding tactic of plunging into water to escape attacking raptors. The European Kingfisher (*Alcedo atthis*) similarly plunges into water (Boag 1982), and it seems likely that all kingfishers would do the same. What these birds might do if attacked away from water is not clear.

Piciformes.—When attacked by raptors, woodpeckers (Picidae) dodge attack by jumping to the opposite side of the trunk on which they are feeding, hence the unusual coding in Appendix I. Furthermore, several species terminate escape by adopting a cryptic posture involving outstretched wings and the flattening of the body against the trunk. Woodpeckers may not seem very cryptically colored, but this posture is effective towards humans (K. A. Sullivan, pers. comm.). The large Pileated Woodpecker may aggressively deter predators as large as Cooper's Hawks (Michael 1921).

Passeriformes.—Flycatchers (Tyrannidae) are a large group with a notable absence of information on escape tactics. This may reflect the fact that many flycatchers do not winter in temperate North America and thus are not present for the "season" during which most observations of escape behavior are made (see above). Perhaps this lack of information also reflects their alert feeding posture, which may deter attacks from predators. Nevertheless, alertness must be backed-up with an ability to escape once attacked. Two observations suggest that flycatchers employ their well-developed aerial maneuvering abilities to avoid capture. The generality of these observations is, however, far from clear.

The larks (Alaudidae) are open-country birds prone to using aerial escape tactics (Appendix I). Horned Larks use a socially coordinated, aerial escape tactic similar to that described for shorebirds, but not as strongly coordinated (pers. obs.). I located no North American observations on Eurasian Skylarks, but observations from their native Europe suggest that solitary skylarks use an aerial climbing strategy to avoid attacking predators. In fact, Solomon (1988) suggested that the singing in which these birds engage (Dean 1989) while pursued by Hobbies (*Falco subbuteo*) acts as a pursuit deterrence signal (cf Caro 1986). Note also that hard-pressed skylarks may seek the refuge of physical objects such as vegetation, and even automobiles (Boyle 1991) and humans (Riols 1990). In general, however, natural history accounts (e.g., Ali and Ripley 1974) and observations in Schluter (1988a) suggest that all larks are primarily aerial escapers.

Swallows (Hirundinidae) are a group of common birds with very few observations; nonetheless, these birds may form a major portion of the diet of falcons (Allen and Knight 1913, Bird and Aubry 1982, Parr 1985). The one available observation suggests that swallows employ an aerial dodging tactic similar to that described for White-throated Swifts.

The crows and jays (Corvidae) may exhibit body-size-dependent escape tactics. The smaller species (jays and magpies) seek woody cover when attacked. American Crows also escape to woody cover, but they may also employ aerial dodging as seen in larger gulls. Ravens, the largest passerine, may aggressively defend themselves from attacks.

The anti-predatory behavior of chickadees and titmice (Paridae) of eastern North America is well characterized (Smith 1991), and all exhibit a woody-cover-dependent escape tactic common to many passerines. The western representatives of this group have not received the same attention, but their behavior (per. obs.) suggests that this basic tactic is employed by all parids. Note also that the ecologically and behaviorally parid-like

Bushtits (Aegithalidae) exhibit very similar escape behavior, and the same probably holds for Verdins (Remizidae; *Auriparus flaviceps*).

I found no observations of escape from attack in the nuthatches (Sittidae), despite their prominence in studies of anti-predatory social behavior (Morse 1977, Waite 1987). B. Enoksson (pers. comm.) indicates that after predatory attack, European Nuthatches (*Sitta europaea*) may be very difficult to locate, even though they may not have left the tree on which they were feeding; in one instance, a nuthatch was found hanging motionless, upside-down on the underside of a branch. Thus I suspect that these birds use a woodpecker-like escape tactic involving tree trunks/branches and probably a cryptic posture. Such a strategy is more clearly the case for the sole representative of the Certhiidae in North America, the Brown Creeper. The woodpecker-like escape tactic in this tree-trunk foraging bird also includes a very effective "terminal" cryptic posture (McClelland 1975).

The two wren species (Troglodytidae) for which I have observations both take woody cover as their escape destination. It seems likely that all wrens would similarly seek vegetation when attacked.

I could locate no observations on escape behavior in the Cinclidae, represented by the American Dipper (*Cinclus mexicanus*). However, it seems likely that they would seek the safety of water if attacked (at least when feeding).

The Muscicapidae are another large group for which there are relatively few observations. The two kinglets exhibit a vegetation-dependent escape tactic very similar to that seen in chickadees. The American Robin also appears largely vegetation-dependent in escape. Note, however, that many members of this group (e.g., robins, bluebirds *Sialia* spp.) sometimes feed far from woody vegetation. Thus there may be more complexity in the escape behavior of these birds than current observations suggest.

All of the Mimidae are closely associated with dense, woody vegetation (Grinnell 1917), and such cover is probably their destination when under predatory attack. My many observations of raptor attacks on Curve-billed Thrashers confirm woody cover as the escape destination for at least one member of this group.

All members of the Motacillidae (wagtails, pipits, etc.), Bombycillidae (waxwings), and Sturnidae (*Sturnus* spp. only) probably exhibit a socially-coordinated aerial escape tactic. This escape tactic has been described many times in the European Starling (Appendix I), although solitarily feeding starlings may seek woody vegetation or other objects when attacked (James 1991). A similar social/solitary dichotomy is evident in the Water Pipit. The Cedar Waxwing is one of the few birds that forages in or on woody vegetation yet uses a socially-coordinated aerial escape tactic when attacked; the Bohemian Waxwing (*B. garrulus*) is undoubtedly very similar.

The few North American representatives of both the Ptilogonatidae (Phainopepla) and Laniidae (shrikes) occur in relatively open, exposed habitats. However, all of these largely solitary birds feed in, or perch on, woody vegetation, and thus probably use a vegetation-dependent escape tactic. Observations confirm this in the shrikes.

Almost all North American vireos (Vireonidae) winter in the neotropics, and thus are largely unrepresented in the escape tactics "literature" (see above discussion of seasonal biases). The Solitary Vireo winters in North America to some extent, and thus is the one member of this group represented in Appendix I. Like the parids and other birds with which it feeds (Gaddis 1980), this vireo seeks dense, woody vegetation when attacked by raptors. Other vireos probably use a similar tactic.

The family Emberizidae comprises relatively diverse but apparently closely-related subfamilies once classified as separate families (Sibley and Ahlquist 1990). However, because these subfamilies are relatively large and distinctive, I consider each separately.

North American warblers (Parulinae), like the ecologically similar vireos, almost all winter in the neotropics and thus have poorly-described escape behavior; the same is true for the few North American tanagers (Thraupinae). However, like the Solitary Vireo, a few warblers winter in mixed species flocks in the southeastern United States (Gaddis 1980). These warblers (Appendix I) all seek dense, woody vegetation when attacked; other warbler species probably do the same.

The large-billed finches comprising the Cardinalinae winter primarily in the neotropics, and thus are also poorly described in terms of escape behavior. However, Cardinals and Pyrrhuloxias, both permanent North American residents, seek woody cover when attacked by raptors. Such an escape tactic may not be observed uniformly in this group; the highly social Dickcissel (*Spiza americana*) probably uses a socially-coordinated aerial escape tactic during the non-breeding season.

The subfamily Emberizinae, comprising buntings, longspurs, New World sparrows, etc., is a large and unusually well-characterized group (relying heavily upon my personal observations, Appendix I). This group is notable for a diversity of escape tactics representative of passerines in general (see also below). Observations suggest a similar diversity for New World blackbirds (subfamily lcterinae), but these few observations probably do not fully characterize this subfamily.

Escape tactics in the Fringillidae (Appendix I) may also be relatively diverse. Represented in Appendix I are herbaceous- and woody-vegetation-dependent escape tactics, as well as the socially coordinated aerial escape tactic. Note also that crossbills exhibit the unusual vegetation-to-air escape tactic described earlier for waxwings (Bombycillidae). Crossbills may not be the only fringillid exhibiting such unusual escape behavior: the highly-coordinated flight and flushing behavior (pers. obs.) of Pine Siskins (*Carduelis pinus*) and Evening Grosbeaks (*Coccothraustes vespertinus*) suggest that arboreal, socially feeding fringillids may generally employ such a strategy.

Also notable in the Fringillidae is an indication of considerable variation in escape behavior within species. For instance, American Goldfinches (and probably redpolls) may exhibit both an aerial and vegetation-dependent escape tactic (Appendix I). Similar "flexibility" is indicated by Lindström (1989) in an Old World fringillid, the Brambling (*Fringilla montifringilla*), which preferentially seeks woody cover if available, but may use an apparently socially coordinated aerial escape tactic if feeding far from such cover.

The ubiquitous House Sparrow, the major representative of the Passeridae in North America, exhibits a woody-cover-dependent escape tactic. Schluter's (1988a) observations on the behavior of African finches suggest that most (if not all) members of this family take woody cover as their escape destination.

SUMMARY OF ESCAPE TACTICS

My goal in this section is to provide some generalizations concerning the nature of escape tactics in North American birds. Given the incomplete coverage of the above survey, I consider these generalizations to be tentative, and offer them mainly as points for further investigation. I organize my discussion around the basic escape destinations.

Vegetation

Woody vegetation.—Perhaps most intuitively, a bird under attack should seek a refuge in which it would be absolutely safe from further attack. The nearest thing to such an impregnable refuge is dense woody vegetation (although *Accipiter* hawks may pursue birds on foot into such cover, Bergstrom 1985; pers. obs.). Thus it is easy to understand why many terrestrial bird species make this their escape destination. Less clear is whether variation in the quality of woody vegetation is important to escape. It seems reasonable that there exists an optimal vegetational density for escape; vegetation too dense cannot be penetrated quickly, and vegetation too sparse offers little protection (especially against *Accipiters*). No work to my knowledge has addressed this issue.

This question of cover density suggests that birds similar in size to their raptorial predators (e.g., grouse, Rock Doves, etc.) would be at a disadvantage in using woody vegetation for escape. These birds might find it difficult to locate cover into which they could flee and not be followed easily by a predator. Thus relatively small birds may be more likely to use woody vegetation for escape, and such is generally apparent in the above survey. However, most of these small "woody-escapers" are passerines, raising the specter of a strong phylogenetic (as opposed to adaptive) component to such a trend (Harvey and Pagel 1991). Note, however, that this trend is also apparent in the Galliformes and within the passerines themselves (e.g., Corvidae, Appendix I). In any case, this pattern deserves greater attention.

Herbaceous vegetation.—Grass-like herbaceous vegetation is often the escape destination of marsh and grassland birds. This does not necessarily reflect a lack of other destinations for escape in such habitats, for many grassland sparrows ignore woody vegetation when fleeing from humans (Pulliam and Mills 1977; Lima and Valone 1991; Watts, in press) and raptors (pers. obs.).

The precise nature of escape tactics based upon herbaceous vegetation is not clear. Since this vegetation probably does not provide the "impregnable" refuge of woody cover (although it may impede attack), an escaping bird's objective is apparently to make difficult further detection by the predator. In other words, these often cryptic birds (Pulliam and Mills 1977) may essentially hide from predators by quickly moving out of danger of being detected again. Such an idea underlies the use of the term "screening cover" in Watts (1990). Presumably, this screening cover must be relatively dense (but not too dense) for effective escape. No study has addressed this directly, but many grassland sparrows seem to seek out relatively dense vegetation (Grzybowski 1983a, b).

Tree trunks.—This destination seems limited entirely to tree-trunk foraging birds: woodpeckers, creepers, and probably nuthatches. These birds dodge attack by "jumping" to the opposite side of the trunk on which they are feeding. Because relatively thick trunks may require a lengthy escape maneuver, and very thin trunks may provide little impedance to predators, there may exist a preferred trunk diameter for escape. No studies examine this possibility, but Sullivan (1984) observed that Downy Woodpeckers abandon thin branches for thicker ones after simulated attacks. In any case, it seems likely that the preferred trunk diameter is a function of body size, with smaller birds preferring thinner trunks.

The cryptic posture terminating escape in many of these "trunk escapers" suggests that tree trunk coloration may be an important determinant of escape. No studies have addressed this possibility.

Air

A variety of birds seek open air (or remain in the air) when under predatory attack (Appendix I). There is considerable variation in aerially-based escape tactics.

Speed-based tactics.—Birds employing speed-based aerial escape tactics attempt to "out-run" a predator, often a relatively slow *Accipiter* hawk. This basic tactic is observed in doves and galliforms. These birds tend to be relatively large, and are therefore swift fliers (Peters 1983). Their size may also preclude the effective use of woody or herbaceous cover for escape. Few, if any, passerines employ this tactic, perhaps due to their generally small size.

Aerial dodging.—Many species too large to have many serious natural predators (e.g., the larger gulls, owls, and corvids) often use a quick, aerial dodge just before predator impact, perhaps to avoid injury more than death per se. However, aerial foragers such as swifts and swallows also appear to use such maneuvering as their major mode of escape. It also seems likely that some sort of last-minute dodge is important for escape in flycatchers. Given this escape tactic, however, exactly what terminates an attack (besides capture) is not clear: why would not a predator attack continually until successful? Predators may terminate attack to locate less alert prey.

Socially-coordinated escape.—Species employing this tactic launch into the air nearly simultaneously and then maneuver (change direction, attitude, etc.) in a highly-coordinated manner (Davis 1980, Potts 1984) while flying in a compact flock. The birds in such a flock act almost as a single behavioral unit during escape. Such a tactic is observed most prominently in several families within the Charadriiformes and Passeriformes, and probably occurs in certain members of the Columbiformes and Anseriformes. Most socially coordinated escapers are small birds (Appendix I), but the gulls and doves using this tactic are relatively large.

Socially coordinated escapers are generally birds of relatively vegetation-free, "exposed" habitats (e.g., beaches, fallow agricultural fields, etc). Some notable exceptions are found in arboreal frugivores/granivores such as waxwings, some fringillids (e.g., crossbills), and Asian Brown-eared Bulbuls (Pycnonotidae; *Ixos amaurotis,* McClure 1957), all of which feed directly on woody vegetation yet do not use it for escape. The reason why these birds use an aerial escape tactic is unclear; perhaps the crowns of the trees in which they feed are not dense enough to offer much protection. To complicate matters further, M. J. DeJong (pers. comm.) reports that certain African bulbuls (*Pycnonotus barabatus* and *Andropadus latirostris*) and the frugivorous Speckled Mousebird (*Colias striatus*) will "drop like rocks" out of fruiting trees into dense herbaceous vegetation upon raptor attack. Clearly, generalizations regarding all arboreal frugivores may be premature.

The nature of this social, aerial strategy is clear, but the reason for its apparent effectiveness (e.g., Buchanan et al. 1988) is not. It seems clear, however, that falcons very rarely dive into a compact flock of maneuvering birds (Rudebeck 1950–1951). Some have speculated (Driver and Humphries 1988) that a diving falcon risks injury due to inadvertent collisions with non-target birds. Whatever the reason for the effectiveness of this tactic, a bird is clearly in great danger should it be separated from the flock (Rudebeck 1950–1951); the "solitary" tactics of aerial climbing, diving into water, etc. (Appendix I) seem relatively ineffective. This raises the interesting question of just how many flock members are necessary for the effective use of this socially coordinated tactic.

Water

Water is a common escape destination in waterbirds representing several orders (Appendix I). Many such birds dive directly into water, whether attacked while flying or on the water's surface. Such water-based tactics are not confined to waterfowl. For instance, kingfishers and isolated shorebirds sometimes use an "aerial plunge" to evade capture. Falcons sometimes force non-water-escapers into water, but such species appear doomed under these circumstances (Hunt et al. 1975).

Several instances have been reported of large fish and sea mammals preying upon diving waterfowl (e.g., Scheffer 1944, Riedman and Estes 1988), but very little is known about underwater escape tactics in subsurface feeding waterfowl. Two reported instances of escape from large fish predators indicate that these birds (an eider duck and an auklet) swim quickly to the surface and then launch into the air. However, the generality of such a tactic is unclear, since humans are not predisposed to observing underwater interactions.

Ground

The hard ground would seem a poor destination for escape, but it is used by at least a few species (e.g., Mourning Doves, European Starlings). The sudden breast-first plunge into the ground associated with this tactic appears similar in effect to an aerial dodge and can be quite effective (pers. obs.). However, there must be a substantial risk of injury associated with this tactic, thus it is most likely a "last-ditch" effort.

Snow

Several boreal birds might conceivably plunge into snow to avoid capture. However, to my knowledge, this has been observed only in the Ruffed Grouse. The reason for the rarity of this tactic is not apparent. However, I suspect that a combination of relatively un-encrusted, deep snow (Huempfner and Tester 1988) and a large body mass (for adequate snow penetration) are needed to make this tactic feasible. This might rule-out a snow-based tactic for small birds, and chronically encrusted snow probably denies this tactic to even very large birds.

VARIABILITY IN ESCAPE BEHAVIOR

Generally speaking, Appendix I indicates relatively little intraspecific variability in escape behavior. This is particularly apparent in vegetation-dependent species. Variability is, however, often observed in socially-coordinated aerial escapers who, when alone, seek vegetative cover, water, etc. to evade capture. Similar variability has also been observed in other aerial escapers (e.g., Columbiformes).

There are several important questions concerning variability in escape behavior. For instance, to what extent is escape behavior variable within a given species? Does such variation represent individual behavioral flexibility or inter-individual variability in behavior? Is there any broad geographical variation in a species' escape behavior? Most observed behavioral variability undoubtedly reflects individual decision making contingent upon the specific situation of the attack. However, observations of escape behavior of two sparrows in response to humans suggest large-scale geographical variability. For instance, in Arizona, Savannah Sparrows and Vesper Sparrows (*Pooecetes gramineus*) show a strong affinity for woody cover when flushed (Pulliam and Mills 1977, Lima and Valone 1991) yet show a marked aversion towards such cover in old-fields in Georgia (B. D. Watts, pers. comm.) and Atlantic coastal dunes (pers. obs.). The generality of such geographical variability in escape behavior, or its genetic/environmental basis, is unknown.

The overall lack of variation in escape tactics apparent in this survey may reflect a subtle bias in the reported observations: virtually all were made in a given species' typical habitat. For instance, longspurs were observed while attacked in open habitats, California Quail were observed in their typically brushy habitats, etc. Studies addressing escape tactics in atypical habitats may yield much insight into flexibility in escape behavior. For example, I once observed a typically cover-dependent White-crowned Sparrow feeding in the open with a flock of Lark Buntings. When the flock suddenly flushed in response to a nearby raptor, the sparrow launched into the air with the buntings in an apparently socially-coordinated fashion before dropping into woody cover over which the flock flew.

ECOLOGICAL IMPLICATIONS: HABITAT SELECTION

Following several authors (Pulliam and Mills 1977, Ekman 1986, Kotler and Brown 1988, Schluter 1988a, Watts 1991), I believe that some of the most important insights to be gained from studies of escape behavior concern patterns of habitat selection. The basic idea here is simple. Much behavioral evidence (Lima and Dill 1990) and some unique data on mortality (Watts 1990) suggest that birds (and animals in general) will not settle in habitats in which they perceive a high risk of predation. Such a perception of high risk undoubtedly occurs in habitats whose structure does not match a given species' basic escape tactic. Thus, understanding escape behavior is a key to understanding the way in which predators (as opposed to predation) influence habitat choice and thus avian ecological systems. This potentially powerful idea remains relatively unappreciated in avian ecology, despite its explicit formulation over 15 years ago in Pulliam and Mills (1977).

Consider birds with woody-vegetation-dependent escape tactics who are not dependent upon such vegetation for food (e.g., most granivores). These birds perceive an increasing risk of predation as they feed farther from woody cover (Caraco et al. 1980, Lima and Dill 1990). Accordingly, on a micro-habitat scale of a few m^2, these birds prefer to feed close to cover (e.g., Grubb and Greenwald 1982, Schneider 1984, Ekman 1987, Lima 1987a, Schluter 1988a, Todd and Cowie 1990). Furthermore, experiments show clearly that woody cover is pivotal in determining the distribution of such birds on the scale of several hectares (Watts 1990, 1991, in press; Lima and Valone 1991). These cover-mediated effects of predators may be evident at a scale of km^2 or larger (e.g., regional/continental, Wiens 1989), depending upon the scale of patchiness in brushy cover.

The influence of predators on the distribution of foliage-gleaning birds is less clear. Since these birds tend to use woody vegetation as both a foraging substrate and refuge from attack, such cover may provide both food and safety. Thus, predators may be of little consequence for habitat selection. However, the within-tree microdistribution of these arboreal birds may reflect small-scale variation in the refuge quality of vegetation (Ekman 1986, 1987). On a larger scale, differences in the refuge quality of various tree species may influence habitat choice on the scale of hectares or larger, especially if particularly safe trees have a limited geographical distribution.

Very little is known about the nature of escape, and associated perceptions of predation risk, in species requiring herbaceous vegetation for escape. However, some evidence suggests that these species may not only avoid woody cover for escape (e.g., Pulliam and Mills 1977; Watts, in press), but also avoid large areas to which such cover is added (Lima and Valone 1991), although this effect could reflect competitive interactions with "woody" species. More research focusing on these and other non-woody species may prove insightful.

One might expect aerially escaping birds to be less restricted in choice of habitat given the "vegetation-independent" nature of their escape tactic. However, this appears not to be the case. Virtually all aerial escapers are characteristic of only sparsely vegetated habitats. Some evidence suggests that socially coordinated aerial escapers may avoid woody vegetation (Lima and Valone 1991) and ignore even nearby cover when attacked (Lima 1990). Some of these "aerial" species avoid woody cover to the extent that observations of them sitting in trees are reported (Potter 1935). A still unresolved question is why such birds might avoid cover. I have suggested (Lima 1990, Lima and Valone 1991) that woody vegetation for these species may simply interfere with their escape, which may require a clear flight path in any one of several directions. It is also possible that these species avoid potentially dangerous, cover-oriented predators by staying clear of cover (Lima 1992).

Always a challenge to generalizations regarding aerial escape are the social, arboreal frugivores/granivores that use a socially coordinated aerial escape tactic (e.g., waxwings, crossbills, etc.). It seems likely that while these species do not avoid trees per se, they may nonetheless avoid feeding in closed-in areas (cf Lima 1990), such as the forest interior, that hinder escape.

One further aerial escape tactic worthy of mention is the gravity-assisted aerial plunge described for the Himalayan Snowcock. This tactic requires a steep slope for success, and Bland and Temple (1990) present evidence that these birds seek-out such slopes during the winter influx of Golden Eagles, their major predatory threat. Thus, on a large geographical scale, this escape tactic may limit snowcocks to mountainous areas. Stempniewicz (1983) also suggested that Dovekies, alcids with a similar gravity-assisted escape tactic, may be limited to breeding on steep slopes.

Birds dependent upon water for escape must presumably remain in close proximity to it for safety. Mayhew and Houston (1989) found that terrestrially feeding Eurasian Widgeons (*Anas penelope*) perceive a greater risk of predation as they feed farther from the water's edge. Bent (1925b) describes evidence that many marine ducks avoid flying over land during daily and migrational movements, perhaps as an anti-predator ploy. Obviously, however, for many waterfowl in most situations, a close association with water is mandatory given a host of anatomical and behavioral traits. Nevertheless, observations in Dekker (1987) and Pöysä (1987) suggest that the presence of deep water is an important determinant of escape, and thus perhaps also a strong determinant of habitat selection in these creatures; Pearse (1939) found that various marine ducks seek deep water when approached by Bald Eagles. Such considerations may also hold for non-aquatic birds that seek water when attacked by predators (e.g., kingfishers and Spotted Sandpipers). If habitat selection in these water-escapers is influenced by the depth of water, then it seems likely that many species may experience a conflict between higher feeding rates in shallow water, and safer feeding sites in deeper water.

MATCHING ESCAPE TACTICS TO HABITATS

I have argued that birds will (all-else-equal) select habitats with broad expanses of open areas, or abundant woody cover, or deep water, etc., based on the way in which habitat structure "matches" their escape tactics. This argument's very simplicity, however, masks some of its more salient features. In particular, the idea that escape tactics must match habitat structure is related to the flexibility of escape behavior in the species in question. For instance, escape in a given species may be so inflexible that the probability of escape (POE) is greatly compromised in any "non-matching" habitat; such species should obviously prefer a matching habitat regardless of the abundance of predators within it. Less obvious, however, is the possibility that even small differences in the POE between habitats can lead to strong preference for the best-matching (highest POE) habitat even under apparently high attack rates in that habitat. The key here is that POEs interact multiplicatively to influence habitat selection (Lima 1992) such that a seemingly small difference in the POE between habitats becomes "magnified" in its effects on habitat selection; this is most important when escape behavior is particularly effective in a given habitat. Thus even birds flexible in escape behavior may be strongly associated with habitats matching their most effective escape tactic. Furthermore, a seemingly paradoxical evolutionary outcome of this phenomenon is that birds may be in the odd position of preferring those habitats containing their co-evolved and presumably most dangerous predators (Lima 1992).

LIFE-HISTORY CORRELATES: TAXONOMIC AND PHYLOGENETIC PERSPECTIVES

A species' escape tactic is only one aspect of its anti-predatory behavioral repertoire, and life-history in general. In short, an escape tactic is one of a suite of life-history traits that determine a species' present-day ecological propensities. My goal in this section is to discuss escape tactics in a broader life-history context.

The following analysis would ideally include all North American bird species. However, the lack of information on escape tactics in many taxonomic groups makes this impossible. Thus my analysis focuses on the emberizine finches, one of the few groups for which there is adequate information. Furthermore, this group of birds exhibits much of the diversity in escape tactics apparent in passerines and terrestrial birds in general (Appendix I). Thus I believe the results below will generalize readily to many other terrestrial taxa.

I first focus on three traits following Pulliam and Mills (1977) and

Grzybowski (1983a): escape tactic, sociality, and habitat vegetational density. Escape tactics for each emberizine species are scored by escape destination as in Appendix I: air (A), herbaceous vegetation (Vh), or woody vegetation (Vw). Species often occurring in large flocks (ca 50 individuals or more) are scored as highly social (H), while those typically social but in smaller flocks (ca 5–20 individuals) are scored as moderately social (M). Species exhibiting low-level sociality (L) usually occur in small flocks (ca 5 individuals or fewer), while those often solitary are scored as S. A species' typical habitat is scored as D for dense vegetation (herbaceous or woody) and E for exposed with sparse and usually short vegetation. A habitat scoring of M signifies moderate habitat exposure: considerable vegetation is present but feeding takes place in relatively exposed, nearby areas.

For several species for which there is no direct information on escape behavior, I have substituted published observations (Pulliam and Mills 1977, Grzybowski 1983a) or my personal observations of "escape" responses to human observers; such behavior seems closely related, in this group at least, to that during actual predatory attack (pers. obs.). Habitat and sociality scores were based primarily upon published observations in Bent (1968), Terres (1980), and others and supplemented with my personal observations whenever such information was lacking. In addition, species exhibiting geographical variability in escape behavior (Savannah and Vesper sparrows) were scored as per the apparently more typical escape tactic.

Table 1 shows each of the North American emberizine finches and how it was scored. Note that almost all of the variability in the focal traits occurs between rather than within recognized genera. Table 2 classifies these species still further by placing each into one of the 36 possible combinations of escape, sociality, and vegetational density. Immediately apparent is a non-random pattern of trait association, with only nine of the 36 cells containing any observations. Of these occupied cells, five contain 37 of the 43 emberizine species in Table 1. These occupied cells may conceivably define four basic suites of correlated traits (Table 3).

What evolutionary forces might favor these basic suites of traits over other possibilities? Pulliam and Mills (1977) suggest that solitary, Type-IV-like (Table 3) grassland sparrows have relatively little to gain from the anti-predatory aspects of sociality (e.g., early detection of predators, Elgar 1989) and rely instead on their cryptic plumage and furtive behavior in avoiding predators (Pulliam and Mills' "solitary cryptic" strategy). Grzybowski (1983a) suggests further that predator detection itself may be difficult in dense grass, thus flocking there may merely enhance detection by predators. It also seems likely that vegetationally dense habitats

TABLE 1
SOME NON-BREEDING SEASON LIFE HISTORY TRAITS OF NORTH AMERICAN EMBERIZINE FINCHES WINTERING (TO SOME EXTENT) NORTH OF MEXICO

	Escape[a]	Sociality[b]	Habitat[c]
Green-tailed Towhee (*Pipilo chlorurus*)	Vw	S	D
Rufous-sided Towhee (*P. erythrophthalmus*)	Vw	S	D
Canyon Towhee (*P. fuscus*)	Vw	L	M
California Towhee (*P. crissalis*)	Vw	L	M
Abert's Towhee (*P. aberti*)	Vw	S	D
Bachman's Sparrow (*Aimophila aestivalis*)	Vw	L	M
Cassin's Sparrow (*A. cassinii*)	Vw?	L?	M
Rufous-winged Sparrow (*A. carpalis*)	Vw	M	M
Rufous-crowned Sparrow (*A. ruficeps*)	Vw	L	M
American Tree Sparrow (*Spizella arborea*)	Vw	M	M
Chipping Sparrow (*S. passerina*)	Vw	M	M
Clay-colored Sparrow (*S. pallida*)	Vw	H	M
Brewer's Sparrow (*S. breweri*)	Vw	M	M
Field Sparrow (*S. pusilla*)	Vw	M	M
Black-chinned Sparrow (*S. atrogularis*)	Vw	M	M
Vesper Sparrow (*Pooecetes gramineus*)	Vh (Vw)	L	M
Lark Sparrow (*Chondestes grammacus*)	Vw	M	M
Black-throated Sparrow (*Amphispiza bilineata*)	Vw	M	M
Sage Sparrow (*A. belli*)	Vw	M	M
Lark Bunting (*Calamospiza melanocorys*)	A	H	E
Savannah Sparrow (*Passerculus sandwichensis*)	Vh (Vw)	L	M
Baird's Sparrow (*Ammodramus bairdii*)	Vh	S	D
Grasshopper Sparrow (*A. savannarum*)	Vh	S	D
Henslow's Sparrow (*A. henslowii*)	Vh	S	D
LeConte's Sparrow (*A. leconteii*)	Vh	S	D
Sharp-tailed Sparrow (*A. caudacutus*)	Vh	L	D
Seaside Sparrow (*A. maritimus*)	Vh	S	D
Fox Sparrow (*Passerella iliaca*)	Vw	S	D
Song Sparrow (*Melospiza melodia*)	Vw	L	D
Lincoln's Sparrow (*M. lincolnii*)	Vw	S	D
Swamp Sparrow (*M. georgiana*)	Vw	L	D
White-throated Sparrow (*Zonotrichia albicollis*)	Vw	M	M
Golden-crowned Sparrow (*Z. atricapilla*)	Vw	M	M
White-crowned Sparrow (*Z. leucophrys*)	Vw	M	M
Harris' Sparrow (*Z. querula*)	Vw	M	M
Dark-eyed Junco (*Junco hyemalis*)	Vw	M	M
Yellow-eyed Junco (*J. phaeonotus*)	Vw	M	M
McCown's Longspur (*Calcarius mccownii*)	A	H	E
Lapland Longspur (*C. lapponicus*)	A	H	E
Smith's Longspur (*C. pictus*)	A	H	E
Chestnut-collared Longspur (*C. ornatus*)	A	H	E
Snow Bunting (*Plectrophenax nivalis*)	A	H	E
McKay's Bunting (*P. hyperboreus*)	A	H	E

TABLE 2

DISTRIBUTION OF EMBERIZINE FINCH SPECIES AMONG THE 36 LIFE HISTORY "COMBINATIONS" DEFINED BY THE ESCAPE DESTINATIONS (3), LEVELS OF SOCIALITY (4), AND HABITAT VEGETATIONAL DENSITY (3) AS PER TABLE 3. ENTRIES ARE THE NUMBER OF SPECIES PLACED IN A GIVEN CATEGORY

	Escape destination								
	Air			Herbaceous veg.			Woody veg.		
	Habitat			Habitat			Habitat		
Sociality	E	M	D	E	M	D	E	M	D
Solitary						5			5
Low					2	1		5	2
Moderate								15	
High	7							1	

block visual contact between would-be flock members, thus negating any potential benefit from the social detection of predators (Elgar 1989). It seems unlikely that the escape tactic used by such birds would, in itself, favor a solitary existence. However, should the herbaceous-vegetation-dependent escape tactic rely upon dense vegetation, then it may indirectly favor or maintain a solitary existence.

The factors favoring the relatively solitary existence of Type III species (Table 3) may not mirror those of Type IV species. In particular, dense woody vegetation is not nearly as visually impairing as dense grass, and thus a lack of visual contact between would-be flock members seems an unlikely reason for a lack of sociality. These birds are also relatively detectable to predators, yet unsociable. I suspect that the impregnable nature of dense woody vegetation effectively thwarts or deters predatory attack. Thus Type III species may experience the costs of sociality (e.g., competition, aggression, etc.) to a much greater extent than potential anti-predatory benefits.

Pulliam and Mills (1977) suggested a "social evasion" strategy for birds of the exposed habitats typical of Type I birds: prey are easily detected by predators, thus sociality is maintained largely by the benefits of a social predator detection system (see also Grzybowski 1983a). This is reasonable, but the highly gregarious nature of Type I birds may largely reflect their socially based escape tactic, which may require many birds to be effective. The relative contribution of predator detection vs escape con-

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[a] Symbols for escape destinations as per Appendix I.

[b] S—largely solitary; L—Low; M—moderate; H—high.

[c] E—exposed; M—moderate density of vegetation; D—dense vegetation.

TABLE 3
POSSIBLE BASIC SUITES OF LIFE HISTORY TRAITS FOR EMBERIZINE FINCHES

Type	Escape destination	Sociality	Habitat density
I	Air	High	Exposed
II	Woody vegetation	Low–moderate	Moderate
III	Woody vegetation	Solitary (largely)	Dense
IV	Herbaceous vegetation	Solitary–low	Dense

siderations in the maintenance of high sociality in these species is unknown, but a stronger role for the latter is suggested by the fact that predator detection levels-off with relatively few (e.g., 6–10) flock members (Lazarus 1979).

Type II species feed in relatively exposed areas in habitats otherwise relatively rich in woody vegetative cover. Escape from predatory attack requires a quick dash to cover, which in turn requires the early detection of predatory attack (Lima 1987b). Thus the benefits of socially based predator detection are probably a major factor maintaining sociality in such species. As noted above, these predator detection benefits level-off at relatively small flock sizes, perhaps explaining the moderate sociality of Type II species. There appears to be no social component to the woody cover-dependent escape tactic, thus post-attack escape considerations may be of little relevance to the maintenance of sociality in Type II species.

The non-random association of traits apparent in Table 2 begs a quantitative comparative analysis. However, the individual species in Table 1 probably do not represent independent units of analysis, since congeneric species vary little in their life-history traits. These complications are best addressed via an explicitly phylogenetic comparative analysis (Brooks and McLennan 1991, Harvey and Pagel 1991). A major impediment to such analyses, however, is the lack of complete, rigorously produced phylogenetic trees. This problem is apparent in the Emberizinae, although some emberizine genera have received excellent coverage (Zink 1982, Zink and Avise 1990). The most comprehensive treatment of this group of birds can be found in Sibley and Ahlquist (1990). Their phylogeny of the Emberizinae (their tribe Emberizini) is shown in Fig. 1. This tree concurs generally in various points of overlap with more limited phylogenetic analyses (Zink 1982, Avise et al. 1980), and despite some reservations concerning DNA hybridization (e.g., Houde 1987, Sarich et al. 1989), it appears to be the best available hypothesis of evolutionary relationships among the Emberizinae. Note, however, that this tree is incomplete and not fully resolved, thus conclusions based on it are tentative.

Fig. 1 indicates the distribution of the basic life-history "types" among

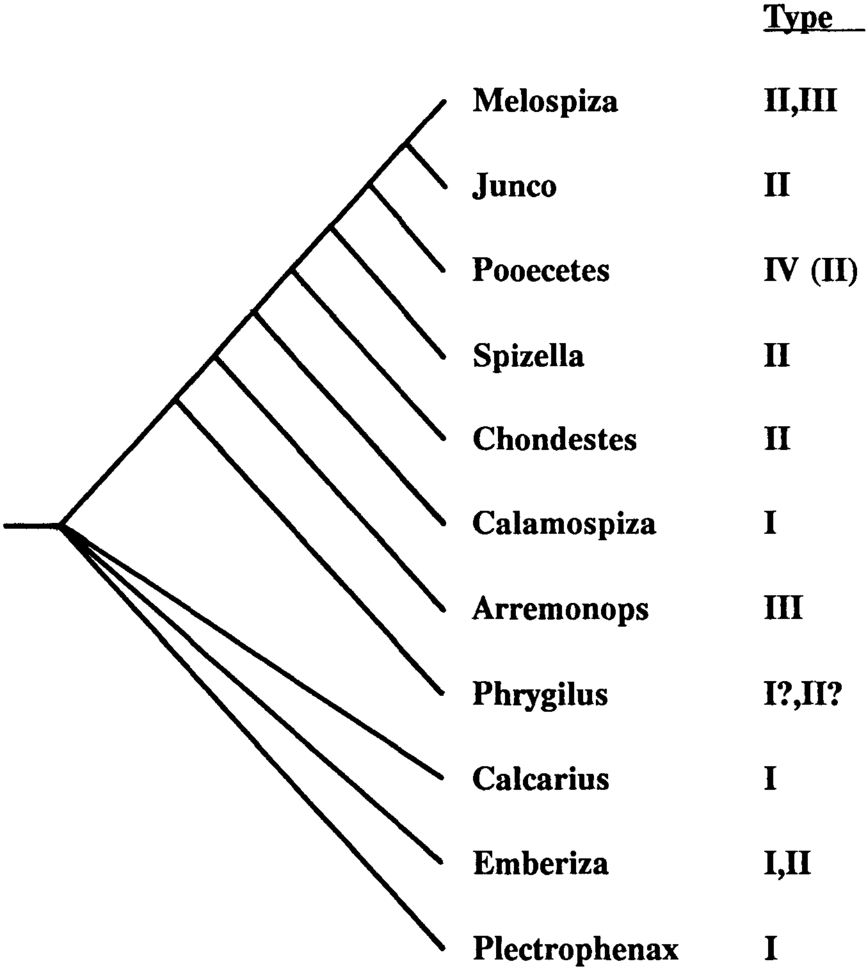

FIG. 1. Hypothesis (tree) of phylogenetic relationships among some emberizine finches. This tree is adapted from a portion of fig. 384 (p. 869) of Sibley and Ahlquist (1990), using genera as the operational taxonomic units (OTU). Basic OTU life-history "types" are characterized as per Table 3 given the information in Table 1. Genera not described in Table 1 were characterized according to available accounts of their natural history: observations in Ali and Ripley (1974) indicate clearly that the Old-World genus *Emberiza* comprises both Type I and II species, while Ridgely and Tudor (1989) indicate clearly that *Arremonops* species of Central and South America exhibit Type III characteristics; further observations in Ridgely and Tudor (1989) suggest (less clearly) that the South American genus *Phrygilus* comprises both Type I and II species. The monotypic genus *Pooecetes* exhibits apparent geographical variation in escape tactics, hence the ambiguity in type assignment (see also Table 1). *Melospiza* sparrows comprise both Type II and III life-histories (Table 1).

the taxa of this phylogenetic tree. Social, aerial escapers (Type I species) cluster at the base of the tree. This suggests that the Type I strategy is the ancestral situation within the Emberizinae, despite the fact that Type II species comprise the largest group within this subfamily (Table 2). This is contrary to the suggestion in Pulliam and Mills (1977) that Type I species (their "social evaders") arose from a generalist emberizine ancestor. Interestingly, the Type I Lark Buntings (*Calamospiza*) may represent a reversal to the ancestral Type I situation from the derived vegetation-dependent (Type II or III?) state; perhaps "phylogenetic inertia" (cf Brooks and McLennan 1991) in the form of a recent Type II or III ancestor explains the fact that this species is one of the few Type I strategists that does not strongly avoid woody cover (Lima 1990).

Most importantly, Fig. 1 suggests that most genera (and species) with vegetation-based escape tactics are the result of an evolutionary radiation from a single common ancestor. Thus, the pattern in Table 2 may merely reflect phylogenetic inertia rather than strong evidence for suites of co-adapted traits (Brooks and McLennan 1991, Harvey and Pagel 1991). However, with additional observations of escape behavior and better phylogenies, future analyses including non-emberizine taxa would probably show patterns of evolutionary convergence similar to that in Table 2, and thus constitute stronger evidence for the suites of traits identified in Table 3. For instance, it is clear that almost all socially coordinated aerial escapers (Appendix I) fit the basic Type I profile, and birds typical of dense vegetation such as wrentits (Muscicapidae) and wrens (Troglodytidae) are probably best described by a Type III or IV strategy. Many woody-cover-dependent passerines such as jays, chickadees, etc., also appear reasonably well described by a Type II strategy. Of course, the inclusion of non-passerines into the analysis would probably identify several additional strategies.

OTHER CORRELATED TRAITS

Escape tactics may be correlated with several other life-history traits in addition to those discussed above. This brief section offers but a few possibilities for future investigation.

Morphology and anatomy.—The shapes of wings and tails, etc., indicate much about the ecological habits of a given bird (Savile 1957). B. D. Watts (pers. comm.) suggests that these morphological traits also covary with escape tactic in some emberizine finches. In particular, he found that woody-cover-dependent species, compared to herbaceous-cover-dependent species, exhibit lower wing aspect ratios, longer tails, and lower relative flight muscle mass and heart mass. These differences presumably correlate with different flight and metabolic requirements during escape.

Similarly, Benkman (1991) shows that emberizine finches have more flight muscle mass relative to their bill size than do cardueline finches (see also Schluter 1988b). He associates this result with differences in the risk of predation in microhabitats frequented by these two groups of birds.

Physiology.—Type I species, in their characteristically exposed habitats, presumably experience a more thermally stressful environment than species more closely associated with vegetation (Grzybowski 1983a). Do Type I species exhibit enhanced abilities to withstand such physiological stress? Are such species affected less by wind than vegetation-dependent species? Do Type I species maintain a greater relative mass of feathers than vegetation-dependent species (cf Faaborg 1988)? Such considerations are important in habitat selection (Huey 1991), and may well be traits that correlate with escape tactics.

Nomadism.—An apparently unnoticed correlate of the socially coordinated aerial escape tactic is nomadism. Among North American emberizines, Snow Buntings, Lark Buntings, and longspurs are well-known for their erratic geographical distribution between years (Root 1988) and within seasons (Grzybowski 1983a, b). These species are closely related (Fig. 1) and thus may exhibit nomadic behavior merely by phylogenetic inertia. However, similar nomadism is also well-known in Rosy Finches (Swenson et al. 1988) and crossbills (Root 1988), two aerially escaping fringillids, as well as in other fringillids (Evening Grosbeaks and Pine Siskins; Yunick 1983) that may also use such an escape tactic. Nomadism is also apparent in waxwings (Bombycillidae; Root 1988) and larks (Alaudidae; Grzybowski 1983a), two apparently distantly-related (Sibley and Ahlquist 1990), aerially escaping groups. Thus, at least in passerines, nomadism appears associated with this escape tactic.

Why would nomadism be associated with the socially coordinated aerial escape tactic? Consider first birds dependent upon vegetation for escape. It seems reasonable that such birds must be familiar with the location and nature of escape cover to ensure their safety (cf Metzgar 1967); such familiarity may be gained only by long-term experience in a given area. For social aerial escapers, refuge from attack is the group itself rather than a spatially-variable entity like vegetation. These Type I birds might experience no "familiarity constraint," and are therefore free to move widely in search of food. Thus this escape tactic may enable these birds to specialize on spatially unpredictable but rich patches of food, much as suggested by Brown (1989) in a temporal context. Of course, nomadism may be only indirectly associated with the social aerial escape tactic if gregariousness is maintained via social enhancement in the location of food (Thompson et al. 1974, Valone 1989) which may be important in nomadic species. Furthermore, Benkman and Pulliam (1988) link nomadic wandering in fringillids to the relatively large size and patchy distribution of the seeds in their diets. They reason that larger seeds provide enough energy such that daily needs can be met quickly once food is located and that the time remaining can be devoted to locating additional sources of food. These explanations are not mutually exclusive, and present an interesting problem in evolutionary biology.

CONCLUSIONS

The birds of North America exhibit diverse escape tactics, and the diversity documented here may well represent only a fraction of the total. In particular, the haphazard nature of literature reports of actual predatory attacks on adult birds has left gaps in the taxonomic survey (Appendix I). The restriction of observations to the non-breeding season also means that escape tactics in neotropical migrants and breeding birds have gone virtually undescribed. This lack of breeding season observations may be particularly problematic in species with precocial young, whose non-breeding-season escape tactic may leave young particularly vulnerable to the attacking predator (e.g., White and Weeden 1966; Sordahl 1981, 1990). Furthermore, there are undoubtedly predator-specific escape tactics that have not been identified in this survey, nor has the nature of geographical and intra-individual variability in escape tactics been determined for any species. These shortcomings can be rectified only with more observations on encounters between predators and their avian prey. I suspect that many such encounters have been witnessed by members of the greater ornithological community, and I encourage the reporting of such observations in the detail suggested by this survey.

It is nonetheless clear that a given "class" of escape tactics requires a certain physical structure(s) within the environment for maximal effectiveness and that a strong factor in habitat choice in many species is the match between its escape tactic and the physical structure of its environment. Of course, a species' escape tactic is but one attribute that will influence habitat choice; foraging abilities, etc., will also be important. Nevertheless, much evidence (Lima and Dill 1990) suggests that the behavior of birds (and other animals) is strongly influenced by a perceived risk of predation. Thus, understanding a species' escape tactic may be crucial to understanding its perception of risk and, therefore, choice of habitat.

Further observations of escape tactics, along with advances in avian phylogenetic systematics, will make possible studies of the evolutionary correlates of escape tactics that are more rigorous than the ones I have described above. These studies may also identify suites of correlated traits in addition to those outlined for emberizine finches and provide much greater insight into the way in which escape tactics influence avian ecological systems in general.

Predation has never been a central focus in avian ecology (Wiens 1989), and perhaps it is true that predation generally does not directly influence the dynamics and structure of avian ecological systems. Nevertheless, this survey presents compelling reasons why predators may still play a major role in avian ecology. If so, then perhaps future treatments of avian natural history (e.g., Ehrlich et al. 1988) will include species-specific accounts of escape tactics in addition to more traditional information.

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APPENDIX I

ESCAPE TACTICS OF SOME NORTH AMERICAN BIRDS

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<tr><td>Podicipediformes: Podicipedidae (1 of 7)</td><td></td><td></td></tr>
<tr><td>Grebe species (small)</td><td>A → W|F|pl Cushing (1939)</td><td></td></tr>
<tr><td>Procellariiformes: Diomedeidae (0 of 3)</td><td></td><td></td></tr>
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<tr><td>Procellariiformes: Hydrobatidae (0 of 6)</td><td></td><td></td></tr>
<tr><td>Pelecaniiformes: Sulidae (0 of 3)</td><td></td><td></td></tr>
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<tr><td>Pelecaniiformes: Anhingidae (0 of 1)</td><td></td><td></td></tr>
<tr><td>Ciconiiformes: Ardeidae (9 of 12)</td><td></td><td></td></tr>
<tr><td>American Bittern (<i>Botarurus lentiginosus</i>)</td><td>V, G → A|M|preceded by “freezing” Bent (1925a)</td><td>706</td></tr>
<tr><td>Least Bittern (<i>Ixobrychus exilis</i>)</td><td>V → Vh|M| on foot Bent (1925a)</td><td>86</td></tr>
<tr><td>Great Blue Heron (<i>Ardea herodias</i>)</td><td>Aggressive display|E|no flight Bayer (1979)</td><td>2390</td></tr>
<tr><td>Great Egret (<i>Casmerodius albus</i>)</td><td>G → A|B Caldwell (1986)</td><td>883</td></tr>
<tr><td>Snowy Egret (<i>Egretta thula</i>)</td><td>G → A|B Caldwell (1986)</td><td>371</td></tr>
<tr><td>Little Blue Heron (<i>E. caerulea</i>)</td><td>G → A|B Caldwell (1986)</td><td>340</td></tr>
<tr><td>Tricolored Heron (<i>E. tricolor</i>)</td><td>G → A|B Caldwell (1986)</td><td>375</td></tr>
<tr><td>Cattle Egret (<i>Bubulcus ibis</i>)</td><td>A, G → A|E|dg Knight (1976), Jennings and Jennings (1982)</td><td>338</td></tr>
<tr><td></td><td>G → A|B Courser and Dinsmore (1971)</td><td></td></tr>
<tr><td>Green-backed Heron (<i>Butorides striatus</i>)</td><td>G → Vh|B Becker and Byers (1976)</td><td>212</td></tr>
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<tr><td>Roseate Spoonbill (<i>Ajaia ajaia</i>)</td><td>Aggressive display|F|no flight Clark (1981)</td><td>1500</td></tr>
<tr><td>Ciconiiformes: Ciconiidae (0 of 1)</td><td></td><td></td></tr>
<tr><td>Anseriformes: Anatidae (12 of 44)</td><td></td><td></td></tr>
<tr><td>Snow Goose (<i>Chen caerulescens</i>)</td><td>W → W|E|dv Bent (1925b)</td><td>2950</td></tr>
<tr><td>Green-winged Teal (<i>Anas crecca</i>)</td><td>W → W|F|dv Dekker (1987)</td><td>341</td></tr>
<tr><td></td><td>A → W, V|F|pl Dekker (1987); K. Winker, pers. comm.</td><td></td></tr>
<tr><td>Mallard (<i>A. platyrhynchos</i>)</td><td>W → W|F|dv Dekker (1987)</td><td>1082</td></tr>
<tr><td></td><td>A → W, V|F|pl Dekker (1987), Beebe and Webster (1985)</td><td></td></tr>
<tr><td>Northern Pintail (<i>A. acuta</i>)</td><td>W → W|F|dv Dekker (1987)</td><td>1011</td></tr>
<tr><td></td><td>A → W, V|F|pl Dekker (1987)</td><td></td></tr>
<tr><td>Blue-winged Teal (<i>A. discors</i>)</td><td>W → W|F|dv Dekker (1987)</td><td>386</td></tr>
<tr><td></td><td>A → W, V|F|pl Dekker (1987)</td><td></td></tr>
<tr><td>Northern Shoveler (<i>A. clypeata</i>)</td><td>W → W|F|dv Dekker (1987)</td><td>613</td></tr>
<tr><td></td><td>A → W, V|F|pl Dekker (1987)</td><td></td></tr>
<tr><td>Gadwall (<i>A. strepera</i>)</td><td>W → W|F|dv Dekker (1987)</td><td>920</td></tr>
<tr><td></td><td>A → W, V|F|pl Dekker (1987)</td><td></td></tr>
<tr><td>American Wigeon (<i>A. americana</i>)</td><td>W → W|F|dv Dekker (1987)</td><td>756</td></tr>
<tr><td></td><td>A → W, V|F|pl Dekker (1987)</td><td></td></tr>
<tr><td>Lesser Scaup (<i>Aythya affinis</i>)</td><td>W → W|F|dv Dekker (1987)</td><td>820</td></tr>
<tr><td></td><td>A → W, V|F|pl Dekker (1987)</td><td></td></tr>
<tr><td>Common Eider (<i>Somateria mollissima</i>)</td><td>W → A|M(seal) Bent (1925b)</td><td>2067</td></tr>
<tr><td>Common Goldeneye (<i>Bucephala clangula</i>)</td><td>A → W|F|pl Bent (1925b)</td><td>900</td></tr>
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<tr><td>Falconiformes: Falconidae (2 of 7)</td><td></td><td></td></tr>
<tr><td>American Kestrel (*Falco sparverius*)</td><td>A → A|A|sp,dg S. L. Lima (SLL), pers. obs.</td><td>116</td></tr>
<tr><td>Merlin (*F. columbarius*)</td><td>A → A|F|steep dives Dekker (1980)</td><td>186</td></tr>
<tr><td>Galliformes: Cracidae (0 of 1)</td><td></td><td></td></tr>
<tr><td>Galliformes: Phasianidae (11 of 20)</td><td></td><td></td></tr>
<tr><td>Gray Partridge (*Perdix perdix*)</td><td>G → Vw|F Shulz (1978)</td><td>390</td></tr>
<tr><td>Ring-necked Pheasant (*Phasianus colchicus*)</td><td>G → Vw|A Alexander (1947)</td><td>1135</td></tr>
<tr><td>Willow Ptarmigan (*Lagopus lagopus*)</td><td>G → Vw^d|F, E|dg White and Weeden (1966)</td><td>559</td></tr>
<tr><td></td><td>G → A|F, E|downslope flight White and Weeden (1966)</td><td></td></tr>
<tr><td>Rock Ptarmigan (*L. mutus*)</td><td>G → Vw|F, E|dg White and Weeden (1966)</td><td>425</td></tr>
<tr><td></td><td>G → A|F, E|downslope flight White and Weeden (1966)</td><td></td></tr>
<tr><td>Ruffed Grouse (*Bonasa umbellus*)</td><td>G → A|A|sp SLL, pers. obs.</td><td>577</td></tr>
<tr><td></td><td>V(exp) → Snow|A|pl Rue (1973), Huempfner and Tester (1988)</td><td></td></tr>
<tr><td>Sage Grouse (Centrocercus urophasianus)</td><td>G → A|E|sp Hartzler (1974)</td><td>343</td></tr>
<tr><td>Wild Turkey (*Meleagris gallopavo*)</td><td>G → Vw|E Thomas et al. (1964)</td><td>5811</td></tr>
<tr><td>Northern Bobwhite (*Colinus virginianus*)</td><td>G → Vw|A Bent (1937, p. 119)</td><td>178</td></tr>
<tr><td></td><td>G → A|B|sp SLL, pers. obs.</td><td></td></tr>
<tr><td>Gambel's Quail (*Callipepla gambelii*)</td><td>G → Vw|B, A Beck et al. (1973), SLL, pers. obs.</td><td>166</td></tr>
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Taxa	Escape tactics[a] and citations	Body mass[b]
California quail (*C. californica*)	G → Vw|A de Fremery (1930)	173
Himalayan Snowcock (*Tetraogallus himalayensis*)	G → A|E|downslope flight Bland and Temple (1990)	2400
Gruiformes: Rallidae (7 of 9)		
Black Rail (*Laterallus jamaicensis*)	G → Vw|M|on foot Bent (1925a)	31.5
Clapper Rail (*Rallus longirostris*)	G → Vh|E, B, A, F De Groot (1927), Bent (1925a) G, W → W|?|dv Bent (1925a)	297
King Rail (*R. elegans*)	Vh → Vh|M Bent (1925a)	361
Virginia rail (*R. limicola*)	G → Vh|M Bent (1925a)	82.0
Sora (*Porzana carolina*)	Vh → Vh|M Bent (1925a) Vh → W|?|dv Bent (1925a)	74.6
Common Moorhen (*Gallinula chloropus*)	Vh → W|?|dv Bent (1925a)	334
American Coot (*Fulica americana*)	W → W|E, G|dv, may also "scoot" on surface De Groot (1927), Sobkowiak and Titman (1989)	642
Gruiformes: Aramidae (0 of 1)		
Gruiformes: Gruidae (0 of 2)		
Charadriiformes: Charadriidae (0 of 9)		
Charadriiformes: Haematopodidae (0 of 2)		
Charadriiformes: Recurvirostridae (1 or 2)		
American Avocet (*Recurvirostra americana*)	G → A|F|scg? Boyce (1985)	316
Charadriiformes: Scolopacidae (15 of 37)		
Lesser Yellowlegs (*Tringa flavipes*)	? → A|?|scg Driver and Humphries (1988)	81.0

APPENDIX I
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Taxa	Escape tactics[a] and citations	Body mass[b]
Spotted Sandpiper (*Actitis macularia*)	G, A → W|F, M|pl Kelso (1926), Stone (1925), Sutton (1925), Martin and Atkeson (1958), E. O. Willis, pers. comm.	40.4
Marbled Godwit (*Limosa fedora*)	G → A|F|scg Boyce (1985), V. Meretsky, pers. comm.	371
Ruddy Turnstone (*Arenia interpres*)	G → A|A|scg Whitfield (1988)	129
Black Turnstone (*A. melanocephala*)	G → A|F|scg Munro (1936), Campbell (1975)	127
Red Knot (*Calidris canutus*)	G → A|F|scg Bijlsma (1990)	137
Sanderling (*C. alba*)	G → A|F|scg B. Kus, pers. comm.	58.8
Semipalmated Sandpiper (*C. pusilla*)	G → A|F|scg Townsend (1930)	28.1
Western Sandpiper (*C. mauri*)	G → A|F|scg Boyce (1985) A → W|F, H|pl Boyce (1985)	23.3
Least Sandpiper (*C. minutilla*)	G → A|F|scg Boyce (1985), Grinnel and Hunt (1929) A → W|F, H|pl Boyce (1985)	20.9
Pectoral Sandpiper (*C. melanotos*)	G → A|F Townsend (1930) A → Vh[d]|F, J|pl Dekker (1980), Pruett-Jones (1980)	73.0
Dunlin (*C. alpina*)	G → A|F|scg, cl Buchanan et al. (1988), Boyce (1985), Bijlsma (1990) A → W|F|pl Buchanan et al. (1988), Boyce (1985)	79.7
Buff-breasteed Sandpiper (*Tryngites subruficollis*)	G → A|F|scg Dekker (1980)	62.0
Short-billed Dowitcher (*Limnodromus griseus*)	G → A|F|cl, dg Dekker (1980) A → W|F|pl Dekker (1980)	114
Red-necked Phalarope (*Phalaropus lobatus*)	G, A → A|F|scg D. Dekker, pers. comm.	33.5
Charadriiformes: Laridae (6 of 39)		

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Taxa	Escape tactics[a] and citations	Body mass[b]
Franklin's Gull (*Larus pipixcan*)	G, A → A|F|scg, dg Dekker (1980), D. Dekker, pers. comm.	280
Bonaparte's Gull (*L. philadelphia*)	G, A → A|F|scg D. Dekker, pers. comm.	212
Ring-billed Gull (*L. delawarensis*)	G, A → A|E|dg Dekker (1980)	519
California Gull (*L. californicus*)	A → A|F|dg Pearse (1937)	609
Glaucous-winged Gull (*L. glaucescens*)	A → A|E|dg SLL, pers. obs.	1010
Glaucous Gull (*L. hyperboreus*)	A → A|F|dg Bent (1938, p. 7)	1413
Charadriiformes: Alcidae (3 of 20)		
Dovekie (*Alle alle*)	G → A^d|G|scg? Stempniewicz (1983)	163
	A → W, G^d|G|downslope flight Stempniewicz (1983)	
Pigeon Guillemot (*Cepphus columba*)	W → W|E|dv Paerse (1937), Pearse (1939)	487
Cassin's Auklet (*Ptychoramphus aleuticus*)	W(submerged) → A|Flounder Scheffer (1944)	188
Columbiformes: Columbidae (3 of 8)		
Rock Dove (*Columba livia*)	G → A|F|scg SLL, pers. obs.	542
	A → V|F Treleaven (1980)	
White-winged Dove (*Zenaida asiatica*)	G → A|F, A|sp,dg Hector (1986), SLL, pers. obs.	153
Mourning Dove (*Zenaida macroura*)	G → A|H, A, F|sp,dg George (1951), Hector (1986), SLL, pers. obs.	119
	A → G|A|pl SLL, pers. obs.	
Cuculiformes: Cuculidae (0 of 6)		
Strigiformes: Tytonidae (0 of 1)		
Strigiformes: Strigidae (1 of 18)		
Short-eared Owl (*Asio flammeus*)	A → A|F|dg Dekker (1980)	347

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Taxa	Escape tactics[a] and citations	Body mass[b]
Caprimulgiformes: Caprimulgidae (0 of 6)		
Apodiformes: Apodidae (1 of 4)		
White-throated Swift (*Aeronautes saxatilis*)	A → A|F|dg Arnold (1942)	32.1
Apodiformes: Trochilidae (1 of 13)		
Costa's Hummingbird (*Calypte costae*)	A → A|Curve-billed Thrasher|dg SLL, pers. obs.	3.1
Coraciiformes: Alcedinidae (1 of 3)		
Belted Kingfisher (*Cerle alcyon*)	A → W|A|pl Bent (1937, p. 119), Kirby and Fuller (1978)	148
Piciformes: Picidae (6 of 22)		
Gila Woodpecker (*Melanerpes uropygialis*)	T → T|A|dg on trunk SLL, pers. obs.	65.0
Red-bellied Woodpecker (*M. carolinus*)	T → T|A|dg on trunk and in flight Saul (1983) Escape terminates with cryptic posture	61.7
Downy Woodpecker (*Picoides pubescens*)	T → T|A|dg on trunk Sullivan (1985) Escape terminates with cryptic posture	27.0
Red-cockaded Woodpecker (*P. borealis*)	T → T|A|dg on trunk Ligon (1970) Escape terminates with cryptic posture	43.6
Northern Flicker (*Colaptes auratus*)	G? → T|A|dg on trunk Bent (1939)	132.0
Pileated Woodpecker (*Dryocopus pileatus*)	T → T|A|dg on trunk Bent (1937, p. 101); Kilham (1958) Aggressive defense|A|on trunk Michael (1921)	287

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<tr><td>Passeriformes: Tyrannidae (2 of 33)</td><td></td><td></td></tr>
<tr><td>Eastern Phoebe (<i>Sayornis phoebe</i>)</td><td>V → G^d|F|dg Bent (1942)</td><td>19.8</td></tr>
<tr><td>Eastern Kingbird (<i>Tyrannus tyrannus</i>)</td><td>V → A^d|F|dg de Kiriline Laurence (1949)</td><td>39.5</td></tr>
<tr><td>Passeriformes: Alaudidae (2 of 2)</td><td></td><td></td></tr>
<tr><td>Eurasian Skylark (<i>Alauda arvensis</i>)</td><td>G → A^d|F|cl Solomon (1988)
G → Humans, Automobiles|F Riols (1990), Boyle (1991)</td><td></td></tr>
<tr><td>Horned Lark (<i>Eremophila alpestris</i>)</td><td>G → A|F|scg SLL, pers. obs.</td><td>31.4</td></tr>
<tr><td>Passeriformes: Hirundinidae (1 of 8)</td><td></td><td></td></tr>
<tr><td>Barn Swallow (<i>Hirundo rustica</i>)</td><td>A → A|F|dg Rudebeck (1950–1951)</td><td>18.6</td></tr>
<tr><td>Passeriformes: Corvidae (4 of 16)</td><td></td><td></td></tr>
<tr><td>Steller's Jay (<i>Cyanocitta stelleri</i>)</td><td>G → Vw|A SLL, pers. obs.</td><td>106</td></tr>
<tr><td>Blue Jay (<i>C. cristata</i>)</td><td>V(exp), G → Vw|A SLL, pers. obs.</td><td>86.8</td></tr>
<tr><td>American Crow (<i>Corvus brachyrhynchos</i>)</td><td>A → Vw|F|dg Dekker (1980)
A → A|F|dg, cl Dekker (1980)</td><td>896</td></tr>
<tr><td>Common Raven (<i>C. corax</i>)</td><td>Aggressive defense|F|in flight Bent (1946)</td><td>1199</td></tr>
<tr><td>Passeriformes: Paridae (3 of 10)</td><td></td><td></td></tr>
<tr><td>Black-capped Chickadee (<i>Parus atricapillus</i>)</td><td>V(exp) → Vw|A Morse (1970)</td><td>10.8</td></tr>
<tr><td>Carolina Chickadee (<i>P. carolinensis</i>)</td><td>V(exp) → Vw|A Morse (1970), Gaddis (1980)</td><td>10.2</td></tr>
<tr><td>Tufted Titmouse (<i>P. bicolor</i>)</td><td>V(exp) → Vw|A Morse (1970), Gaddis (1980)</td><td>21.6</td></tr>
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Taxa	Escape tactics[a] and citations	Body mass[b]
Passeriformes: Remizidae (0 of 1)		
Passeriformes: Aegithalidae (1 of 1)		
Bushtit (*Psaltriparus minimus*)	V(exp) → Vw|A Miller (1922)	5.3
Passeriformes: Sittidae (0 of 4)		
Passeriformes: Certhiidae (1 of 1)		
Brown Creeper (*Certhia americana*)	? → T|S|dg on trunk Bent (1948) Escape terminates with cryptic posture	8.4
Passeriformes: Troglodytidae (2 of 9)		
Cactus Wren (*Campylorhynchus brunneicapillus*)	G → Vw|A SLL, pers. obs.	38.9
House Wren (*Troglodytes aedon*)	? → Vw|A K. Sullivan, pers. comm.	10.6
Passeriformes: Cinclidae (0 of 1)		
Passeriformes: Muscicapidae (3 of 19)		
Golden-crowned Kinglet (*Regulus satrapa*)	V(exp) → Vw|A SLL, pers. obs.	6.2
Ruby-crowned Kinglet (*R. calendula*)	V(exp) → Vw|A Morse (1970)	6.6
American Robin (*Turdus migratorius*)	A, G → Vw|A|dg Dekker (1980), SLL, pers. obs.	77.3
Passeriformes: Mimidae (1 of 10)		
Curve-billed Thrasher (*Toxostoma curvirostre*)	G → Vw|A SLL, pers. obs.	79.4
Passeriformes: Motacillidae (1 of 5)		
Water Pipit (*Anthus rubescens*)	A → A|F|scg Bent (1938, p. 77) A → A|F|cl Bent (1938, p. 77)	20.9

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<tr><th>Taxa</th><th>Escape tactics[a] and citations</th><th>Body mass[b]</th></tr>
<tr><td>Passeriformes: Bombycillidae (1 of 2)</td><td></td><td></td></tr>
<tr><td>Cedar Waxwing (<i>Bombycilla cedrorum</i>)</td><td>V(exp?), A → A|A|scg Meyerriecks (1957)</td><td>31.9</td></tr>
<tr><td>Passeriformes: Ptilogonatidae (0 of 1)</td><td></td><td></td></tr>
<tr><td>Passeriformes: Laniidae (2 of 2)</td><td></td><td></td></tr>
<tr><td>Northern Shrike (<i>Lanius excubitor</i>)</td><td>V(exp) → Vw|F Cade (1967)</td><td>65.6</td></tr>
<tr><td>Loggerhead Shrike (<i>L. ludovicianus</i>)</td><td>V(exp) → Vw|A D. Dekker, pers. comm.</td><td>47.4</td></tr>
<tr><td>Passeriformes: Sturnidae (1 of 2)</td><td></td><td></td></tr>
<tr><td>European Starling (<i>Sturnus vulgaris</i>)</td><td>G, A → A|F, A|scg Tinbergen (1951), SLL, pers. obs.
G → Vw|A|feeding alone SLL, pers. obs.</td><td>82.3</td></tr>
<tr><td>Passeriformes: Vireonidae (1 of 11)</td><td></td><td></td></tr>
<tr><td>Solitary Vireo (<i>Vireo solitarius</i>)</td><td>V(exp) → Vw|A Gaddis (1980)</td><td>16.6</td></tr>
<tr><td>Passeriformes: Emberizidae Parulinae (5 of 51)</td><td></td><td></td></tr>
<tr><td>Orange-crowned Warbler (<i>Vermivora celata</i>)</td><td>V(exp) → Vw|A Gaddis (1980)</td><td>9.0</td></tr>
<tr><td>Yellow-rumped Warbler (<i>Dendroica coronata</i>)</td><td>V(exp) → Vw|A Morse (1970), SLL, pers. obs.</td><td>12.3</td></tr>
<tr><td>Yellow-throated Warbler (<i>D. dominica</i>)</td><td>V(exp) → Vw|A Gaddis (1980)</td><td>9.4</td></tr>
<tr><td>Pine Warbler (<i>D. pinus</i>)</td><td>V(exp) → Vw|A Gaddis (1980)</td><td>11.9</td></tr>
<tr><td>Black-and-white Warbler (<i>Mniotilta varia</i>)</td><td>V(exp) → Vw|A Gaddis (1980)</td><td>10.8</td></tr>
<tr><td>Passeriformes: Emberizidae Thraupinae (0 of 4)</td><td></td><td></td></tr>
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Taxa	Escape tactics[a] and citations	Body mass[b]
Passeriformes: Emberizidae Cardinalinae (2 of 10)		
Northern Cardinal (*Cardinalis cardinalis*)	G → Vw|A SLL, pers. obs.	44.7
Pyrrhuloxia (*C. sinuatus*)	G → Vw|A SLL, pers. obs.	35.5
Passeriformes: Emberizidae Emberizinae (19 of 44)		
Green-tailed Towhee (*Pipilo chlorurus*)	G → Vw|A SLL, pers. obs.	29.4
Rufous-sided Towhee (*P. erythrophthalmus*)	G → Vw|A SLL, pers. obs.	40.5
Canyon Towhee (*P. fuscus*)	G → Vw|A SLL, pers. obs.	44.4
California Towhee (*P. crissalis*)	G → Vw|A, F, B Davis (1957)	52.9
American Tree Sparrow (*Spizella arborea*)	G → Vw|A, F SLL, pers. obs.	20.1
Field Sparrow (*S. pusilla*)	G → Vw|A SLL, pers. obs.	12.5
Black-throated Sparrow (*Amphispiza bilineata*)	G → Vw|A SLL, pers. obs.	13.5
Lark Bunting (*Calamospiza melanocorys*)	G → A|H, F, A|scg SLL, pers. obs.	37.6
Savannah Sparrow (*Passerculus sandwichensis*)	A → Vh|F, S Dekker (1980), Cade (1967)	20.1
Grasshopper Sparrow (*Ammodramus savannarum*)	V(exp) → Vh|A Bent (1968), SLL, pers. obs.	17.0
Song Sparrow (*Melospiza melodia*)	G → Vw, Vh|A SLL, pers. obs.	20.8
White-throated Sparrow (*Zonotrichia albicollis*)	G → Vw|A SLL, pers. obs.	25.9
Golden-crowned Sparrow (*Z. atricapilla*)	G → Vw|A Bent (1968), Cushing (1939)	28.8
White-crowned Sparrow (*Z. leucophrys*)	G → Vw|A, F SLL, pers. obs.	28.1

APPENDIX I
CONTINUED

Taxa	Escape tactics[a] and citations	Body mass[b]
Dark-eyed Junco (*Junco hyemalis*)	G → Vw|A SLL, pers. obs.	19.8
Yellow-eyed Junco (*J. phaeonotus*)	G → Vw|A K. Sullivan, pers. comm.	20.4
Lapland Longspur (*Calcarius lapponicus*)	G → A|A|scg Grzybowski (1983a), SLL, pers. obs.	27.3
	A → Vh^d|J|solitary Pruett-Jones (1980)	
Chestnut-collared Longspur (*C. ornatus*)	G → A|F|scg Grzybowski (1983a), SLL, pers. obs.	18.9
Snow Bunting (*Plectrophenax nivalis*)	G → A|F|scg D. Dekker, pers. comm.	42.2
Passeriformes: Emberizidae Icterinae (5 of 18)		
Red-winged Blackbird (*Agelaius phoeniceus*)	G → A|F, H|scg SLL, pers. obs.	52.6
Meadowlark (*Sturnella* spp.)	G, A → Vh|F SLL, pers. obs.	89.0
Common Grackle (*Quiscalus quiscula*)	G → Vw|A|feeding alone SLL, pers. obs.	114
Brown-headed Cowbird (*Molothrus ater*)	G → Vw|A|solitary? Pettingill (1976)	43.9
"Blackbirds" (spp. ?)	A → Vh, cattle|F Dekker (1988)	
	G → A|F|scg D. Dekker, pers. comm.	
Passeriformes: Fringillidae (6 of 14)		
Rosy Finch (*Leucosticte arctoa*)	? → A|A|scg(?) Twining (1940)	26.7
House Finch (*Carpodacus mexicanus*)	G → Vw|A SLL, pers. obs.	21.4
Red Crossbill (*Loxia curvirostra*)	V(exp?) → A|F, A|scg? C. Benkman, pers. comm.	36.5
White-winged Crossbill (*L. leucoptera*)	V(exp?) → A|F, A|scg? C. Benkman, pers. comm.	26.6
Common Redpoll (*Carduelis flammea*)	? → A|S|scg? Munro (1930) Note: escape to woody cover is probably preferred in this species	13.0

APPENDIX I
CONTINUED

Taxa	Escape tactics[a] and citations	Body mass[b]
American Goldfinch (*C. tristis*)	G → Vh, Vw[d] | S Cade (1967), A. Middleton, pers. comm. G → A | S | scg? A. Middleton, pers. comm.	12.9
Passeriformes: Passeridae (1 of 2)		
House Sparrow (*Passer domesticus*)	G → Vw | A Barnard (1980), SLL, pers. obs.	27.7

[a] Each observation is given in a three-part code (with occasional notes) as described in text. For example, the code "A → W|F|pl" indicates that a bird attacked in the air plunged into water (its escape destination), and that the predator was a falcon. For species exhibiting multiple escape tactics, that listed first is apparently the preferred tactic. Code abbreviations are as follows. Places of attack or escape destinations: A—Air, G—Ground, relatively free of vegetation, T—Tree trunk, V—Vegetation (Vh—herbaceous (non-woody) vegetation, Vw—woody vegetation (e.g., brush), V(exp)—exposed (typically woody) vegetation offering little protection from predators), W—Water. Types of predators: A—*Accipiter* hawk, B—*Buteo* hawk, E—Eagle, F—Falcon (large), H—Northern Harrier, G—Gull (large), J—Jaeger, M—Mammal (typically a canid), S—Shrike. Common escape behaviors: cl—attempt to out-climb a predator in aerial pursuit. This typically involves a solitary or isolated prey individual. dg—dodge to avoid capture just before impact with predator; performed as an aerial maneuver unless indicated otherwise. dv—dive into water, either from the air or from surface of water. pl—high-speed plunge into escape destination; this abbreviation is used for tactics other than those involving woody vegetation. scg—attacked individuals escape as a socially-coordinated group. This applies only to aerially-escaping species. sp—prey uses superior speed to out-distance the predator.

[b] Body masses (in grams) as given by Dunning (1984); values averaged across sexes in dimorphic species. Body masses for a few species are not available.

[c] Numbers indicate a coverage of "n of the m" species in the family (or subfamily) in question.

[d] Observation made during or close to the breeding season.