

Risk in mobbing for solitary and colonial swallows

CHARLES R. BROWN*† & JOHN L. HOOGLAND†

*Department of Biology, Princeton University, Princeton, New Jersey 08544 U.S.A.

†Appalachian Environmental Laboratory, University of Maryland, Frostburg, Maryland 21532 U.S.A.

Abstract. Barn swallows (*Hirundo rustica*) often nest solitarily and are ecologically similar to colonially nesting cliff swallows (*H. pyrrhonota*). Northern rough-winged swallows (*Stelgidopteryx serripennis*) also nest solitarily and are ecologically similar to colonially nesting bank swallows (*Riparia riparia*). We investigated risk-taking in the mobbing of predators for these four species of North American swallows. We presented model owl and weasel predators and examined tendencies of individuals to dive at these predators during mobbing. Individuals of the two solitary species were significantly more likely to dive at predators than were individuals of the two colonial species. Since diving may be risky, we suggest that solitary species take greater per capita risks in mobbing than do colonial species. The reduced risk of falling victim during mobbing may be a benefit of group living that is perhaps independent of the effectiveness of mobbing.

Reduced predation is an important benefit of group living for some animals (Alexander 1974). Animals in groups often detect approaching predators sooner than do solitary animals because overall group vigilance increases as the number of individuals scanning for predators rises (e.g. Pulliam 1973; Siegfried & Underhill 1975; Hoogland 1979; Lazarus 1979; Bertram 1980; Caraco et al. 1980). Enhanced predator detection may then lead to mobbing, a behaviour in which group members attempt either to assault physically or to distract and confuse an approaching predator (e.g. Horn 1968; Cully & Ligon 1976; Smith & Graves 1978; Rood 1983; Shields 1984). In some cases, mobbing effectiveness seems to increase with the number of mobbers (Hoogland & Sherman 1976; Robinson 1985).

Presumably, mobbing involves some risk to participants since predators sometimes seize mobbers who come too close (e.g. Cade 1967; Denson 1979). Risk, but also mobbing effectiveness, probably increases the closer a mobber approaches a predator. Thus, a mobber is faced with choosing a distance from which to mob that optimizes mobbing effectiveness, while minimizing personal risk.

The distance at which to mob, and thus the degree of risk-taking, could be related to the number of participating mobbers. Individuals

mobbing as a group might have two options which are unavailable to individuals mobbing alone. Relative to a solitarily mobbing individual, a group mobber (1) could increase its distance from the predator and rely on a large group's physical or vocal conspicuousness to bewilder a predator, or (2) it could decrease its distance from the predator, using the confusion created by a large group to sneak up on and physically assault the predator. In the former case, the degree of personal risk is reduced since distance from the predator is increased. In the latter case, risk might also be reduced through selfish herd effects. Individuals of species mobbing solitarily, on the other hand, might have only one option: approach predators closely to deter them more effectively, in the absence of any accompanying generalized group commotion. Individuals mobbing in groups might therefore have a lower per capita risk of falling victim themselves than ones mobbing singly, even though mobbing effectiveness might be equal or, in some cases, greater for group mobbers.

In this study we examined whether individuals mobbing in groups tended to increase or decrease their distance from a predator, relative to individuals mobbing solitarily, and whether the degree of risk-taking might be greater for individuals that mob solitarily. We studied four species of North American swallows (Hirundinidae) that mob predators. Our approach was to present artificial predators to these birds while they were nesting,

† Present address: Department of Biology, Yale University, P.O. Box 6666, New Haven, Connecticut 06511, U.S.A.

and compare responses of the social species that mobbed in groups with those of the solitary species that mobbed singly.

METHODS

Study Animals and Study Areas

The four species of swallows that we studied can be grouped as closely related pairs. Each pair consists of two species that are ecologically similar but that differ in their degree of sociality.

Barn swallow/cliff swallow

The congeneric barn (*Hirundo rustica*) and cliff (*H. pyrrhonota*) swallows build mud nests on vertical rock and cliff faces, on bridges and buildings, and in highway culverts throughout much of North America. Both species are aerial insectivores, and in many areas they feed and nest together. Barn swallows are often solitary, and single breeding pairs occur commonly in many areas. Barn swallow colonies usually contain 2–15 nests; colonies that contain more than 15 nests are rare (e.g. Snapp 1976; Brown, personal observation). Barn swallow colonies apparently now occur in response to relatively recent, human-caused increases in suitable nesting substrates such as buildings and culverts (Snapp 1976), although originally the bird was mostly solitary (Dawson 1897; Betts 1916; S. Speich, personal communication). Since barn swallow 'colonies' are probably evolutionarily quite recent, we believe that the behaviour of this species is characteristic of solitarily living swallows. Cliff swallows, on the other hand, are highly colonial and apparently have always been so (e.g. Sharpe & Wyatt 1885; Bent 1942; Erskine 1979). Single nests are rare, and colonies may contain up to 3000 nests (Brown 1985).

Barn and cliff swallows were studied at two sites: in June and July, 1975, near Laramie, Albany County, Wyoming and near Walden, Jackson County, Colorado; and in June and July 1984, in Keith and Garden Counties, Nebraska. Birds studied in Wyoming and Colorado all nested on artificial structures such as bridges and buildings; those studied in Nebraska nested on both artificial structures and natural cliff sites.

Northern rough-winged swallow/bank swallow

Northern rough-winged (*Stelgidopteryx serripennis*) and bank (*Riparia riparia*) swallows are burrow-nesting species that occur throughout much of North America. Nest burrows are placed in the sides of sandy banks or cliffs, often along rivers or lakes. At present, many northern rough-winged and bank swallows nest in roadcuts or in commercial sand and gravel pits. Northern rough-winged swallows nest solitarily (Lunk 1962). Sometimes up to 10 pairs will nest in the same bank face (Brown, personal observation), but such aggregations are rare. Bank swallows, however, occur in large colonies of up to 1000 nests (e.g. Beecher et al. 1981); isolated nests are unusual. In some areas, northern rough-winged and bank swallows nest and feed together.

Northern rough-winged and bank swallows were studied in June and July, 1972–1973 and 1977, near Ann Arbor, Washtenaw County, Michigan. In this area both species nested primarily in commercial sand and gravel pits.

Predator Presentation Procedures

We used life-like predator models in an attempt to standardize predator presentations between different sites. For barn and cliff swallows, we used stuffed and rubber great horned owls (*Bubo virginianus*). For northern rough-winged and bank swallows, we used a stuffed long-tailed weasel (*Mustela frenata*) (Hoogland & Sherman 1976). Weasels are known predators of both bank and northern rough-winged swallows (Lunk 1962). Although great horned owls have not been observed preying on barn swallows, these owls are known predators of cliff swallows in our Nebraska study area where swallow remains have been found in owl pellets (Sally Gaines, personal communication). Both barn and cliff swallows responded vigorously to model owls, and we concluded that owls elicit natural mobbing behaviour from these species. Cliff swallows' responses to other avian predators such as black-billed magpies (*Pica pica*) and American kestrels (*Falco sparverius*) were similar to their responses to our model owl.

The owl model was tied to a stick 2.5 m above the ground. The owl and stick were placed as close as possible to the entrances of culverts or buildings containing barn and cliff swallow nests or on top of cliffs and bridges under which the birds nested. We placed the owl and then withdrew as quickly as possible and observed the birds' responses. Owls were presented once at each single barn swallow

nest, once at each site containing more than one barn swallow nest, and once at each cliff swallow colony. Since each colony or single nest received only one predator presentation, all presentations were statistically independent. In the case of cliff swallows, which usually detected the owl as soon as it was placed, we observed responses for 5 min before removing the owl. In the case of barn swallows, which often were not present at a nest when the owl was placed, we observed responses for 5 min after at least one bird had returned to the nesting site. At some barn swallow nests the owl was present for up to 10 min before the nest owners arrived and appeared to detect the simulated predator.

The weasel was introduced by hand into active northern rough-winged and bank swallow nest burrows (Hoogland & Sherman 1976). Each bank swallow colony and each northern rough-winged swallow nest received only one predator presentation, so all presentations were statistically independent. The weasel was left in each nest for 5 min after the birds' first response. For bank swallows, the weasel was introduced into centrally located burrows where mobbing intensities were greatest (Hoogland & Sherman 1976).

Predator presentations were done only when barn and northern rough-winged swallow nests contained eggs or nestlings or when more than half of all cliff and bank swallow nests in the colonies contained nestlings. This was to ensure that the birds' responses to predators in general would be maximal at the time we measured them (e.g. Smith & Graves 1978).

Although few birds were colour-marked, in most cases owners of threatened nests probably responded to our model predators. For solitary barn and northern rough-winged swallows, only nest owners were likely to encounter the model predator because few, if any, other birds were present. For colonial cliff swallows, the model owl, which was large and highly visible, was placed in locations so that it would 'threaten' as many different nest owners as possible. Since most cliff swallow colonies in our study areas were large (see Brown 1985), at least some nest owners were likely to be present at a colony virtually all the time and thus would encounter the owl. For colonial bank swallows, Hoogland & Sherman (1976) previously showed, with colour-marked birds, that owners of threatened nests usually initiate mobbing responses.

RESULTS AND DISCUSSION

We first examined whether differences existed in the mobbing distances of the solitary versus colonial species of swallows. We then used mobbing distance to infer mobbing risk, in the absence of any information on a mobber's probability of falling victim during (rarely seen) actual predator attacks. It proved impractical to estimate the distances from the predator for birds swirling above our models, so instead we scored only whether responses included dives by mobbers at the predator. A dive would typically occur as a bird flying 2–3 m above and to the side of the predator would make a sudden, rapid swoop downward to pass within inches of the predator's head. After passing by the predator, the mobber would gain its original altitude and then repeat the procedure. Mobbers that were not diving would circle loosely or swirl in coordinated waves above and to the sides of the model owl or in front of the model weasel, alarm-calling frequently. In the case of bank and northern rough-winged swallows, in which the bank surface afforded perching space near the weasel, we included landings within 2 m of the weasel as high-risk behaviour. We included these landings because perching within 2 m of a swift-moving adult weasel seems as potentially risky as diving at it.

Results of presentations at 25 barn swallow nests or colonies, at 29 cliff swallow colonies, at 50 northern rough-winged swallow nests, and at 34 bank swallow colonies (Table I) show that solitarily mobbing barn and northern rough-winged swallows dived and landed near the predator significantly more often than did the group mobbing cliff and bank swallows. Barn swallows were the most vigorous mobbers; some individuals dived repeatedly at the model owl for several minutes. Bank and cliff swallows seldom dived; instead they milled and swirled around the predator. Mobbing bank swallows typically formed a doughnut-shaped vortex that swirled near a predator (Hoogland & Sherman 1976). Mobbing actions of cliff swallows were less coordinated than those of bank swallows, with most cliff swallows milling overhead in a disorganized fashion.

These results (Table I) indicate that solitary barn and northern rough-winged swallows approach predators more closely than do colonial cliff and bank swallows. These colonial swallows apparently rely on a large group's commotion to deter predators, and individuals rarely approach a predator

Table I. Number of predator presentations (*N*) and number of occasions where at least one dive or one instance of landing near the predator was observed in four species of swallow

Species	<i>N</i>	Diving or landing near*	No diving or no landing near*
Barn swallow	25 nests/colonies	23	2
Cliff swallow	29 colonies	2	27
		$\chi^2 = 38.9, P < 0.001$	
Northern rough-winged swallow	50 nests	17	33
Bank swallow†	34 colonies	2	32
		$\chi^2 = 9.1, P < 0.01$	

* 'Landing near' only included for northern rough-winged swallow and bank swallow.

† Bank swallow trials from 11 colonies were ones also reported in Hoogland & Sherman (1976).

closely. Risk-taking is thus greater for individuals of the solitarily mobbing barn and northern rough-winged swallows than for individuals of the group mobbing cliff and bank swallows.

Limited evidence suggests that this same pattern holds among other North American swallows. Purple martins (*Progne subis*) dive close to predators such as fox squirrels (*Sciurus niger*) when mobbing (Brown 1984; personal observation). Tree swallows (*Tachycineta bicolor*) dive at predators such as dogs and prairie falcons (*Falco mexicanus*), and also dive at people when mobbing (R. Cohen, personal communication; Sheppard 1977). Both martins and tree swallows, at least historically, before the installation of back-yard bird-houses, were largely solitary. In contrast, in the violet-green swallow (*Tachycineta thalassina*), which reportedly is colonial in part of its range (Brown 1983), we have found no reports of diving at nest predators during mobbing, although violet-greens do dive at nesting site competitors such as acorn woodpeckers (*Melanerpes formicivorus*) (Brown, personal observation).

More vigorous attempts to deter predators and increased mobbing risk per individual may be necessary in solitarily nesting species for two reasons. First, there are few or no nesting conspecifics nearby and thus there is no possibility of a coordinated group mobbing effort, nor is mobbing enhanced through the summation of many individuals all actively defending their own nest (e.g. Horn 1968; Shields 1984). Second, solitary individuals are unable to 'hide' their nest among other nests through the selfish herd effect (Hamilton 1971), and thus an approaching predator is more likely to zero in on a given individual's nest when that individual nests alone.

In one of the few previous comparative studies examining mobbing behaviour in gregarious and non-gregarious species, and in contrast to our results reported here, Cully & Ligon (1976) reported that solitary scrub jays (*Aphelocoma coerulescens*) mobbed owl predators less vigorously than did social Mexican jays (*A. ultramarina*). However, Cully & Ligon apparently did not present predators near the nests of the jays, and therefore a comparison of their results with ours for swallows is difficult.

We suggest that an important benefit of coloniality could be reduced per capita risk in the mobbing of predators. Although reduced per capita risk might be automatic for group mobbers simply because a group dilutes each individual's chance of being preyed upon, we have shown here that group mobbers also, and perhaps more importantly, reduced their degree of risk by increasing their distance from the predator. This could be a benefit of group living irrespective of whether mobbing succeeds in deterring predators more reliably in colonies. Reduced risk in mobbing is part of a suite of benefits associated with predator avoidance in groups, but one that has not been explicitly stated or examined until now.

ACKNOWLEDGMENTS

Mary Bomberger Brown conducted most of the Nebraska predator presentations, and assisted in many other important ways. Cathy Boersma, Carol Brashears, Rachel Budelsky, and Laurie Doss also assisted in the field in 1984. Paul Sherman helped gather the bank swallow data in 1972-1973. Brown received financial support from

a National Science Foundation Predoctoral Fellowship, Princeton University, the Chapman Fund of the American Museum of Natural History, the Bache Fund of the National Academy of Sciences, Sigma Xi, Alpha Chi, and Raymond and Kathryn Brown. Hoogland received financial support from the National Science Foundation and the University of Michigan. John Janovy, Jr and the University of Nebraska-Lincoln provided use of the facilities at the Cedar Point Biological Station. For helpful comments on the manuscript we are grateful to M. Beecher, H. Power, P. Sherman and W. Shields.

REFERENCES

- Alexander, R. D. 1974. The evolution of social behavior. *A. Rev. Ecol. Syst.*, **5**, 325-383.
- Beecher, M. D., Beecher, I. M. & Lumpkin, S. 1981. Parent-offspring recognition in bank swallows (*Riparia riparia*): I. Natural history. *Anim. Behav.*, **29**, 86-94.
- Bent, A. C. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. *U.S. Natl Mus. Bull.*, **179**, 463-483.
- Bertram, B. C. R. 1980. Vigilance and group size in ostriches. *Anim. Behav.*, **28**, 278-286.
- Betts, N. DeW. 1916. A recent instance of the nesting of barn swallows on cliffs. *Wilson Bull.*, **28**, 72-73.
- Brown, C. R. 1983. Vocalizations and behavior of violet-green swallows in the Chiricahua Mountains, Arizona. *Wilson Bull.*, **95**, 142-145.
- Brown, C. R. 1984. Vocalizations of the purple martin. *Condor*, **86**, 433-442.
- Brown, C. R. 1985. The costs and benefits of coloniality in the cliff swallow. Ph.D. thesis, Princeton University.
- Cade, T. J. 1967. Ecological and behavioral aspects of predation by the northern shrike. *Living Bird*, **6**, 43-86.
- Caraco, T., Martindale, S. & Pulliam, H. R. 1980. Avian flocking in the presence of a predator. *Nature, Lond.*, **285**, 400-401.
- Cully, J. F. & Ligon, J. D. 1976. Comparative mobbing behavior of scrub and Mexican jays. *Auk*, **93**, 116-125.
- Dawson, W. L. 1897. Natural breeding haunts of the barn swallow. *Auk*, **14**, 95-96.
- Denson, R. D. 1979. Owl predation on a mobbing crow. *Wilson Bull.*, **91**, 133.
- Erskine, A. J. 1979. Man's influence on potential nesting sites and populations of swallows in Canada. *Can. Field Nat.*, **93**, 371-377.
- Hamilton, W. D. 1971. Geometry for the selfish herd. *J. theor. Biol.*, **31**, 295-311.
- Hoogland, J. L. 1979. The effect of colony size on individual alertness of prairie dogs (*Sciuridae: Cynomys* spp.). *Anim. Behav.*, **27**, 394-407.
- Hoogland, J. L. & Sherman, P. W. 1976. Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. *Ecol. Monogr.*, **46**, 33-58.
- Horn, H. S. 1968. The adaptive significance of colonial nesting in Brewer's blackbird (*Euphages cyanocephalus*). *Ecology*, **49**, 682-694.
- Lazarus, J. 1979. The early warning function of flocking in birds: an experimental study with captive quelea. *Anim. Behav.*, **27**, 855-865.
- Lunk, W. A. 1962. The rough-winged swallow *Stelgidopteryx ruficollis* (Vieillot), a study based on its breeding biology in Michigan. *Publ. Nuttall Ornithol. Club*, **4**, 1-155.
- Pulliam, H. R. 1973. On the advantages of flocking. *J. theor. Biol.*, **38**, 419-422.
- Robinson, S. K. 1985. Coloniality in the yellow-rumped cacique as a defense against nest predators. *Auk*, **102**, 506-519.
- Rood, J. P. 1983. Banded mongoose rescues pack member from eagle. *Anim. Behav.*, **31**, 1261-1262.
- Sharpe, R. B. & Wyatt, C. W. 1885. *A Monograph of the Hirundinidae or Family of Swallows, Vol. 1*. London: Taylor & Francis.
- Sheppard, C. D. 1977. Breeding in the tree swallow, *Iridoprocne bicolor*, and its implications for the evolution of coloniality. Ph.D. thesis, Cornell University.
- Shields, W. M. 1984. Barn swallow mobbing: self-defence, collateral kin defence, group defence, or parental care? *Anim. Behav.*, **32**, 132-148.
- Siegfried, W. R. & Underhill, L. G. 1975. Flocking as an anti-predator strategy in doves. *Anim. Behav.*, **23**, 504-508.
- Smith, M. J. & Graves, H. B. 1978. Some factors influencing mobbing behavior in barn swallows (*Hirundo rustica*). *Behav. Biol.*, **23**, 355-372.
- Snapp, B. D. 1976. Colonial breeding in the barn swallow (*Hirundo rustica*) and its adaptive significance. *Condor*, **78**, 471-480.

(Received 25 February 1985; revised 21 August 1985; MS. number: A4494)