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The risk of predation favors cooperation among breeding prey

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Empirical studies have shown that animals often focus on short-term benefits under conditions of predation risk, which reduces the likelihood that they will cooperate with others. However, some theoretical studies predict that animals in adverse conditions should not avoid cooperation with their neighbors since it may decrease individual risks and increase long-term benefits of reciprocal help. We experimentally tested these two alternatives to find out whether increased predation risk enhances or diminishes the occurrence of cooperation in mobbing, a common anti-predator behavior, among breeding pied flycatchers, *Ficedula hypoleuca*. Our results show that birds attended mobs initiated by their neighbors more often, approached the stuffed predator significantly more closely, and mobbed it at a higher intensity in areas where the perceived risk of predation was experimentally increased. This study demonstrates a positive impact of predation risk on cooperation in breeding songbirds, which might help to explain the emergence and evolution of cooperation.

Key words: cooperation, predation risk, social behavior, pied flycatcher

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Predation is one of the main factors responsible for mortality in the wild.[1] To enhance chances of survival, prey individuals often join together to mob a predator by cooperatively attacking it.[2,3] Mobbing activities of prey usually cause the predator to vacate the area and increase the probability that the predator will not return to the area where it has been unsuccessful in obtaining prey.[5] Thus, mobbing reduces the threat to nearby prey individuals and allows them to resume daily activities.[6] Beside these benefits, mobbing incurs costs and there appears to be a group size effect in mobbing, which indicates the importance of cooperation among prey individuals in driving predators away.[7,8]

It has been long assumed that organisms are less cooperative in stressful environmental conditions. Since participation in a cooperative behavior such as mobbing is costly over a short-time scale, animals often value smaller, immediate benefits over large, future benefits, thus inhibiting cooperation under adverse conditions.[9] However, there are examples showing that the occurrence of positive interactions among organisms may be enhanced when living in physiologically stressful environments.[10-12] Increasing empirical evidence suggests a correlation between adverse conditions and cooperative behavior,[13,14] but it is still not known whether adverse conditions play a causal role in the evolution of cooperation because experimental support is lacking.

In our study we found that breeding pied flycatchers were more willing to cooperate with their neighbors after many consecutive encounters with predators that increased their perceived risk of predation. These birds were more willing to mob at their neighbors' nests (**Fig. 1**) and mobbed more intensely in areas with an increased predation risk than birds unexposed to predators. Moreover, in areas with a higher perceived predation risk, birds approached predators at their neighbors' nests more closely. Field studies suggest that mobbing during nest defense increases birds' fitness despite of the immediate risks.[1,8] Since mobbing in a group enhances these fitness benefits, this helps explain why birds mob cooperatively.[5] Through cooperation, prey individuals might significantly intensify their effect on the behavior of predators and alleviate the risks associated with

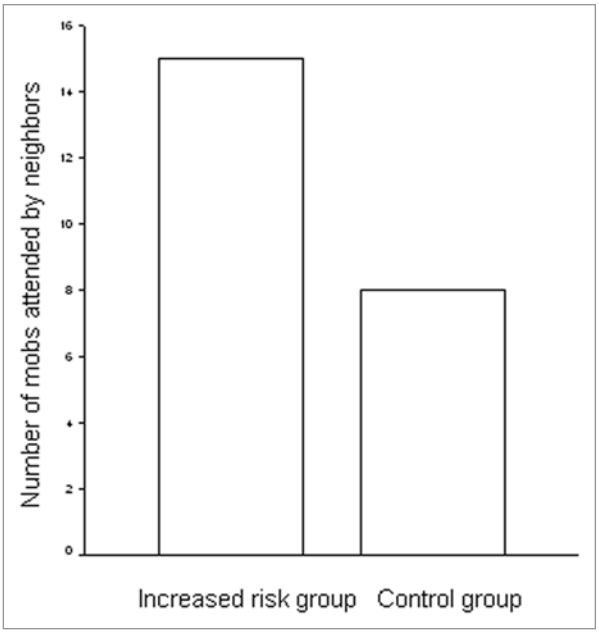

Figure 1. Number of mobs attended by neighboring pied flycatchers in experimental and control groups during test trials. The results show that birds in the increased risk group were more willing to mob a stuffed tawny owl, a common predator of small birds in northern Europe, at their neighbors' nests than the birds in the control group. To increase the perceived risk of predation in the experimental group, the owl was repeatedly placed in each breeding territory of pied flycatchers for 2 h on each of 5 days before testing trials, while a stuffed mistle thrush, *Turdus viscivorus*, was presented in the vicinity of each pair of the birds in the control group.

engaging in mobbing, which might make mobbing in groups profitable even under increased predation risk.

We also found that birds that had received mobbing assistance from neighbors at their own nests were more likely to mob at the nests of neighbors in the future. This result is consistent with previous studies showing that breeding birds engage in reciprocal cooperation when mobbing.[15-19] Reciprocal cooperation produces benefits for participants only when they interact with other co-operators.[20] In our study participants interacted during the course of relatively short breeding season, which appeared to be long enough to establish reciprocal interactions. Together with the previous results revealing that pied flycatchers that encountered predators more frequently were more willing to support their neighbors, who, as a result, were more willing to join these mobs in the future, our results support the theoretical prediction[21-23] and suggest that birds facing a risky environment can reduce their individual risks by cooperating with others. We show experimentally that the risk of predation can have a direct effect on cooperation, which might help to explain the origin and evolution of cooperation. However, more data are badly needed to demonstrate how adversity and uncertainty of environmental conditions might improve fitness prospects for cooperating individuals in mutualistic cooperation based on the principles of reciprocity in different taxa.

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