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In Focus

Featured Articles in This Month's *Animal Behaviour*

Ants Mark Violators for Policing

Policing is a familiar mechanism for maintaining cooperative behaviour in human societies; it is perhaps less well known that this mechanism also operates in other animal societies. In some species of social Hymenoptera, for example, workers physically attack other workers that selfishly attempt to produce their own eggs, and by such policing keep the colony focused on cooperatively aiding the queen's reproduction. Queens themselves rarely participate in policing, at least not in species with large colony sizes, where the actions of a single queen would presumably be relatively ineffective against thousands of workers. Queens can nevertheless affect the outcome of policing by directing the policing efforts of their workers, as shown in a study in this issue (pp. 597–603) by Adrian A. Smith, Bert Hölldobler and Jürgen Liebig of Arizona State University.

Smith and colleagues studied the desert ant *Aphaenogaster cockerelli*, which lives in colonies typically consisting of a single queen and 2000–9000 workers. Previous research on this species had shown that both queens and nonreproductive workers attack workers that produce eggs, and had implicated cuticular hydrocarbons as a cue that singles out such reproductive workers for attack. Thus, unusually for this type of colony organization, queens in this species take some direct part in policing. In the present study, Smith and colleagues show that queens also take an indirect part in policing, by using a second signal, obtained from their Dufour's glands, to mark reproductive workers for attack by other workers.

Smith and colleagues found that when queens encountered a reproductive worker, they would hold the worker while flexing their abdomens under their bodies so as to direct the tip of the abdomen towards the worker (Fig. 1). Additional compounds appeared on the queen's abdomen after such aggressive episodes, and these were shown by gas chromatography to be consistent with compounds present in the queen's Dufour's gland (an abdominal gland associated with the sting apparatus). Queens were found to have more compounds in their Dufour's glands than either reproductive or nonreproductive workers, with a higher proportion of methyl-branched hydrocarbons. Thus the compounds in the queen's Dufour's glands appear to be distinctive.

To test for the effects of Dufour's gland compounds on worker policing behaviour, nonreproductive workers were treated with the contents of Dufour's glands from queens, reproductive workers and nonreproductive workers. Those treated with contents of Dufour's glands from queens received substantially more aggression

Figure 1. An *Aphaenogaster cockerelli* queen (at left) attacks and prepares to mark a reproductive worker. Photo: Adrian A. Smith.

from other workers than those treated with contents of worker Dufour's glands. Specifically, workers treated with queen Dufour's gland contents were bitten, held and pulled, and in one case killed, by other workers.

A previous case exists in which reproductives in a queenless ant were shown to use Dufour's gland contents to mark subordinates for aggression, but this appears to be the first case where this behaviour has been demonstrated in ant queens. Presumably, marking troublemakers for policing by others is a more efficient way of suppressing worker reproduction than is direct policing by the queen herself. This increased efficiency potentially comes at some cost: queens that had attacked and marked workers were often then attacked themselves, suggesting that they may have contaminated themselves with their own Dufour's gland secretions. The balance of costs and benefits of this marking behaviour merits further investigation.

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Call Diversity in Killer Whales

Behavioural variation within a species helps our understanding of the evolution of behavioural patterns. Animal vocalizations lend themselves particularly well to measuring behavioural variation because they are relatively easy to quantify. To gain insights into the mechanisms and selection pressures that drive variation in animal vocalizations, we need to distinguish the different levels at which such variation can occur. Thus, dialects represent differences between neighbouring groups of potentially interbreeding individuals while geographical variation refers to differences over long distances between populations that normally do not interbreed.

The rich vocal repertoire of killer whales consists of clicks, whistles and calls, and is subject to many sources of variation. Killer whales are widely distributed throughout the world's oceans and different populations vary in their dietary specialization, feeding strategies and social structure. In the North Pacific alone, scientists distinguish three ecotypes of killer whale: residents, offshores and transients. Residents live in large stable social groups and feed on fish. The characteristics of offshores are less well known but they also live in large groups and are probably fish specialists. By contrast, transients primarily hunt sea mammals and live in smaller and less stable social groups. Furthermore, the social structure of resident killer whale groups is nested and complex. The basic social unit is the matriline, containing a matriarch and up to four generations of her descendants, who always travel together. Several related matrilines that associate frequently and share a dialect of stereotyped calls constitute a pod. Clans consist of pods that share some of the calls in their repertoire, and populations or communities contain one or more associating clans.

Scientists hypothesize that divergence in vocal repertoires of stereotyped calls between pods happens gradually over generations. As the different matrilines spend less time together, random call mistakes and innovations accumulate through vertical cultural transmission and the vocal repertoires of pods within a clan gradually diverge. This suggests that more distant common maternal ancestry between pods will be associated with fewer shared calls. Indeed, earlier studies have shown that matrilines with similar vocal repertoires are more closely related than matrilines that share only a few calls, but this is consistent with both cultural and genetic lineages. Could divergence in vocal repertoires at a higher structural scale, between different populations of killer whales, be explained by the accumulation of random errors and innovations through vertical cultural transmission?

In the present issue (pp. 587–595), scientists from several countries join together to analyse long-term databases of calls recorded in four distinct populations of resident killer whales in the North Pacific: Southern Residents from southern British Columbia and Washington State, Northern Residents from central British Columbia and southeastern Alaska, Alaskan Residents from southern Alaska and Kamchatkan Residents from eastern Kamchatka (Fig. 2). Olga Filatova (Moscow State University, Russia), Volker Deecke (University of St Andrews, U.K.), John Ford (Fisheries and Oceans Canada, Nanaimo, Canada), Craig Matkin (North Gulf Oceanic Society, Alaska, U.S.A.), Lance Barrett-Lennard (Vancouver Aquarium Marine Science Centre and University of British Columbia, Canada), Mikhail Guzeev (St Petersburg State University, Russia), Alexandr Burdin (Kamchatka Branch of The Pacific Institute of Geography FEB RAS, Russia) and Erich Hoyt (Whale and Dolphin Conservation Society, U.K.) examined the geographical variation of single- and two-voiced calls, referred to as monophonic and biphonic calls, respectively, in their article. The former contain only a low-frequency component while the latter have an additional high-frequency component.

Figure 2. Killer whale pod in eastern Kamchatka. Photo: T. Ivkovich.

The authors found that within each of the four populations, the diversity of single-voiced calls was significantly higher than the diversity of two-voiced calls. Furthermore, single-voiced calls were equally diverse within and between populations while two-voiced calls were significantly less diverse within than between populations for all pairwise comparisons. These results are consistent with findings from earlier studies on the intensity, directionality and usage of single- and two-voiced calls. They provide further evidence for differences in functional significance and principles of evolution that are shared by all four populations of North Pacific killer whales. Taken together, all these findings suggest that the long-range two-voiced calls function as identifiers of group affiliation and help whales to monitor the position of group members over distances of 10–16 km. By contrast, the function of the short-range single-voiced calls is less clear but, like whistles, such calls might be used by killer whales for short-range communication over 5–9 km.

Intriguingly, single-voiced calls were more diverse and two-voiced calls less diverse in larger populations. For human languages, larger population size is a significant predictor of a greater sound diversity among language speakers. Therefore, the evolution of single-voiced calls in killer whales may be driven by stochastic processes similar to those affecting the evolution of human sounds. By contrast, the lower diversity of two-voiced calls in larger populations may be the result of directional selection driven by an increased need for vocal identifiers when the population size is larger. Surprisingly, there was no evidence that the diversity of two-voiced calls increased with increasing approximate geographical distance between pairs of populations as would be expected if similarity between populations reflected their ancestry. However, the long-distance movements of killer whales could easily disturb the ancestral geographical structure.

Overall, the results of this study suggest that the evolution of vocal repertoires is a complex process that involves the interaction of genetic and cultural inheritance, directional and nondirectional change. Future studies of genetic and acoustic similarity across killer whale populations are likely to provide more insights.

Ana Sendova-Franks
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