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Reduced social-information provision by immigrants and use by residents following dispersal

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Greater access to social information is a proposed benefit of group living [1]. However, individuals vary in the quantity and quality of information they provide [2], and prior knowledge about signaller reliability is likely important when receivers decide how to respond [3]. While dispersal causes regular changes in group membership [4], no experimental work has investigated social-information provision and use in this context. We studied sentinel behaviour following immigration in a habituated population of wild dwarf mongooses (*Helogale parvula*) [5]; sentinels (raised guards) use various vocalisations to provide social information [5,6]. Recent immigrants acted as sentinels rarely and significantly less often than residents, limiting their role as social-information providers. Even when recent immigrants acted as social-information providers, foragers responded to them less than they did to residents. Several months after arrival, immigrants had increased sentinel contributions, and foragers no longer responded differently to sentinel activity by former immigrants and residents. Our results raise questions about the assumed social-information benefits associated with increased group size.

In a range of social mammals and birds, individuals adopt raised positions to look out for predators [6]; these ‘sentinels’ (Figure 1A) provide two main types of social information. Alarm calls warn of danger, and likely reduce predation risk; surveillance calls inform about sentinel presence, identity and height, and offer an estimate of current risk, thus enabling groupmates to optimize the foraging–vigilance trade-off (see [5]). Sentinel behaviour is also particularly tractable for field-based

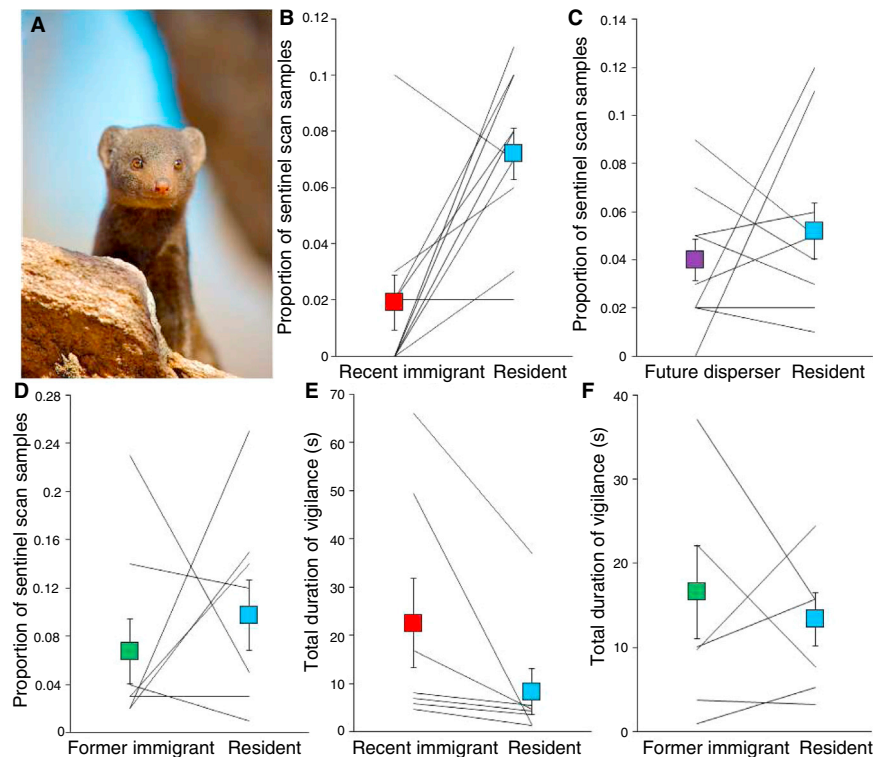


Figure 1. Provision of social information by sentinels, and its use by foragers, in relation to dwarf mongoose dispersal.

(A) A dwarf mongoose acting as a sentinel (raised guard) when it provides social information using vocalisations. Compared with residents (blue squares), dispersers were (B) significantly less likely to act as sentinels in the month after immigrating into a new group (red square; $N=10$), but did not differ in their likelihood of acting as a sentinel either (C) prior to emigration (purple square; $N=10$) or (D) five months after immigration (green square; $N=8$). Shown in (B–D) are the mean daily proportions of scan samples in which a matched pair of individuals in the same group acted as a sentinel (connected by solid lines) and the overall mean for each residence status (solid squares) \pm SE. Compared with the playback of sentinel surveillance calls from residents (blue squares), playback of those from immigrants resulted in foragers exhibiting (E) significantly more vigilance in the month after the immigration event (red square; $N=7$), but (F) the same level of vigilance after at least five months of residence by an immigrant in a new group (green square; $N=6$). Shown in (E,F) are the values for the same focal individuals in the two treatments (connected by solid lines) and the overall treatment mean (solid squares) \pm SE.

data collection and experimental manipulation [5,6], making it an excellent model for considerations of social-information provision and use.

Using long-term life-history data and natural observations of dwarf mongoose behaviour (see Supplemental Experimental Procedures), we first investigated whether immigrants differed from residents of equivalent dominance status in their likelihood of acting as a sentinel and thus their availability as social-information providers. In the month immediately after arrival in a new group, immigrants acted as sentinels rarely and significantly less often than residents (Wilcoxon signed-rank test: $W=2$, $N=10$, $P=0.017$; Figure 1B), limiting their provision of social

information. Immigrants might potentially be generally less cooperative individuals. But, prior to emigration, future dispersers did not differ from others in their natal group in sentinel contributions ($W=23$, $N=10$, $P=1$; Figure 1C). Alternatively, recent immigrants might conduct little sentinel activity because of the likely lower relatedness shared with their new groupmates compared to that with individuals in their natal group. However, five months after arrival and with no further changes in group composition, former immigrants had increased sentinel contributions to a level comparable with that of residents ($W=8$, $N=8$, $P=0.675$; Figure 1D).

Another possibility for the initial low level of sentinel behaviour is that new



arrivals choose to help less when their groupmates are unfamiliar, increasing contributions as familiarity increases over time. Finally, the explanation may be that dispersal is costly; while prospecting alone, individuals do not gain group benefits such as reduced predation risk and increased foraging time and efficiency [7]. Indeed, dwarf mongooses suffer reductions in body mass between emigration and immigration (Figure S1). Since many cooperative acts, including sentinel behaviour, are state-dependent [2], immigrants in the early stages of settlement may be unable to reach the required state for helping, or may show a strategic reduction in cooperation while lost body mass is recouped.

Foragers are known to reduce their own anti-predator vigilance when there is a sentinel, relying more on the social-information provider to survey the environment and warn of danger [5,6]. However, the extent of this vigilance reduction likely depends on sentinel identity [5]. We therefore experimentally mimicked the presence of different dwarf mongoose sentinels with playbacks of their surveillance calls, to investigate the response of foraging individuals to immigrants and matched-status residents as social-information providers. Foragers responded significantly less to surveillance calls from recent immigrants (within one month of their arrival) compared with those from resident group members; they invested more in personal vigilance in the former treatment (Wilcoxon signed-rank test, duration of vigilance: $W=0$, $N=7$, $P=0.016$, Figure 1E; number of look-ups: $W=27$, $N=7$, $P=0.042$). However, foragers no longer responded differently to the surveillance calls of immigrants and residents once the former had been in their new group for five months (duration of vigilance: $W=10$, $N=6$, $P=0.971$, Figure 1F; number of look-ups: $W=8$, $N=6$, $P=0.892$).

There are several potential explanations for the experimental results. Greater vigilance in response to recent immigrants could represent social monitoring of unfamiliar individuals; same-sex immigrants can threaten the social-hierarchy position of subordinate group members [8]. This is unlikely here, however, as the dominant female was the focal individual in all playback trials.

If dwarf mongoose vocalisations contain a group signature (as found in other cooperatively breeding species [9]), then the calls of recent immigrants may be ignored initially if they sound different. Establishing this would require acoustic analysis over long periods, which has not been attempted so far. The greater vigilance seen when recent immigrants act as sentinels could also result from foragers choosing to rely less on these social-information providers than resident groupmates in the same role.

A reduced reliance could arise if immigrants were inherently less reliable individuals; animals are known to track reliability [3]. However, immigrant dwarf mongooses often arrive from neighbouring groups (see Supplemental Information), so likely have similar knowledge of local predators. Moreover, dispersers did just as much sentinel duty in their previous groups as residents (Figure 1C). Alternatively, a reduced reliance could result if receivers value the information from recent immigrants less than that from residents. A lower valuing of information from recent immigrants might stem from a lack of available knowledge about them; it may be beneficial to ignore social information from unfamiliar individuals, instead relying more heavily on personal information. This initial lack of knowledge is likely exacerbated by the low frequency of sentinel behaviour performed by recent dwarf mongoose immigrants (Figure 1B), which limits opportunities to learn about them. After lengthier group membership, immigrants increase their contributions to sentinel behaviour (Figure 1D), providing residents with opportunities to accumulate knowledge about their social-information quality. Perhaps because of these repeated interactions, foragers no longer differentiated between resident groupmates and former immigrants as social-information providers once the latter had been resident for several months (as predicted by recent theory [10]).

Our study offers rare empirical evidence that the provision and use of social information is affected by dispersal events. Moreover, it highlights that the benefits accrued from the addition of a new group member are less than would be expected from a simple increase in group size, at least initially. Since existing group members are likely to suffer costs from the arrival of new individuals, in terms of shared resources and increased

competition, accurate assessment of counteracting benefits is crucial for a full understanding of social evolution.

SUPPLEMENTAL INFORMATION

Supplemental Information including one figure, one table and experimental procedures can be found with this article online at <https://doi.org/10.1016/j.cub.2017.10.045>.

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