

species, early eye evolution has the potential to rapidly go from blur to clarity.

#### References

1. Arendt, D. (2008). The evolution of cell types in animals: emerging principles from molecular studies. *Nat. Rev. Genet.* 9, 868–882.
2. Arendt, D., Tessmar, K., de Campos-Baptista, M.I., Dorrestijn, A., and Wittbrodt, J. (2002). Development of pigment-cup eyes in the polychaete *Platynereis dumerilii* and evolutionary conservation of larval eyes in Bilateria. *Development* 129, 1143–1154.
3. Serb, J.M., and Oakley, T.H. (2005). Hierarchical phylogenetics as a quantitative analytical framework for evolutionary developmental biology. *BioEssays* 27, 1158–1166.
4. Lucas, R.J., Hattar, S., Takao, M., Berson, D.M., Foster, R.G., and Yau, K.-W. (2003). Diminished pupillary light reflex at high irradiances in melanopsin-knockout mice. *Science* 299, 245–247.
5. Arendt, D., Tessmar-Raible, K., Snyman, H., Dorrestijn, A.W., and Wittbrodt, J. (2004). Ciliary photoreceptors with a vertebrate-type opsin in an invertebrate brain. *Science* 306, 869–871.
6. Kozmik, Z., Ruzickova, J., Jonasova, K., Matsumoto, Y., Vopalensky, P., Kozmikova, I., Strnad, H., Kawamura, S., Piatigorsky, J., Paces, V., et al. (2008). Assembly of the cnidarian camera-type eye from vertebrate-like components. *Proc. Natl. Acad. Sci. USA* 105, 8989–8993.
7. Suga, H., Schmid, V., and Gehring, W.J. (2008). Evolution and functional diversity of jellyfish opsins. *Curr. Biol.* 18, 51–55.
8. Erclik, T., Hartenstein, V., Howard, D., Lipshitz, H.D., and McInnes, R.R. (2008). Conserved role of the *Vsx* genes supports a monophyletic origin for bilaterian visual systems. *Curr. Biol.* 18, 1278–1287.
9. Eakin, R.M., and Brandenburger, J.L. (1980). Unique eye of probable evolutionary significance. *Science* 211, 1189–1190.
10. Arendt, D., and Wittbrodt, J. (2001). Reconstructing the eyes of Urbilateria. *Phil. Trans. R. Soc. Lond. B* 356, 1545–1563.
11. Nilsson, D.-E. (1994). Eyes as optical alarm systems in fan worms and ark clams. *Phil. Trans. R. Soc. Lond. B* 346, 195–212.
12. Jarman, A.P., Grell, E.H., Ackerman, L., Jan, L.Y., and Jan, Y.N. (1994). *atonal* is the proneural gene for *Drosophila* photoreceptors. *Nature* 369, 398–400.
13. Holmberg, K. (1977). The cyclostome retina. In *Handbook of Sensory Physiology, Vol. VIII/5*, F. Crescitelli, ed. (Berlin: Springer), pp. 47–66.
14. Lamb, T.D., Collin, S.P., and Pugh, E.N., Jr. (2007). Evolution of the vertebrate eye: opsins, photoreceptors, retina and eye cup. *Nat. Rev. Neurosci.* 8, 960–975.
15. Lacalli, T.C. (2004). Sensory systems in *amphioxus*: A window on the ancestral chordate condition. *Brain Behav. Evol.* 64, 148–162.

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## Sensory Ecology: Noise Annoys Foraging Bats

Traffic noise reduces foraging time and effort in greater mouse-eared bats, presumably by masking rustling sounds made by moving arthropods. Anthropogenic noise is becoming a major concern in conservation biology.

Gareth Jones

We are acutely aware of the difficulties involved in holding conversations next to busy roads. The sound of passing traffic makes communication problematic. Such problems are not restricted to humans — there is increasing evidence that hearing is affected by traffic noise in a wide range of animals. Noise not only affects individuals receiving signals: the signalling animals may alter signal design to cope with masking, so that the signal stands out against background noise [1]. This can be achieved in several ways. For example, nightingales occupying territories exposed to traffic noise sing louder on weekdays (when traffic noise is louder) than on weekends [2]. Common marmosets increase signal duration in noise, because longer sounds are easier to hear [3]. Great tits produce shorter songs, sing more rapidly, and use higher frequencies in urban environments than in forests [4] to enhance signal transmission in noisy environments.

These examples show how noise pollution can influence acoustic communication. A new study by Schaub *et al.* [5] shows how traffic noise can influence foraging behaviour in animals that find their food by listening for the sounds that their prey produce. The authors worked on the greater mouse-eared bat, *Myotis myotis*, a species that often gleans beetles, mole-crickets, spiders and centipedes from the ground (Figure 1). The sensory basis of prey detection in greater mouse-eared bats is well understood [6,7]. The bats use echolocation to find aerial prey, but echolocation is ineffective when prey are amongst vegetation, because echoes from the vegetation overlap with echoes from the prey, making detection difficult. In vegetated habitats, the bats find their food by reducing the volume of their echolocation calls and instead listening for the rustling sounds made by movements of their prey. Arthropods that make louder rustling sounds are more likely to end up eaten by greater mouse-eared bats [8].

Because the bats find prey on the ground by listening for prey-generated sounds, potentially the cues emitted by the prey might be masked by the sound of traffic, and prey detection in noisy habitats might be compromised severely. The movement of ground beetles in vegetation produces a series of broadband clicks, with peak amplitude around 12 kHz [9]. Traffic noise contains considerable energy at this frequency [5], so masking is highly likely.

To test the hypothesis that the foraging behaviour of greater mouse-eared bats is altered under traffic noise, Schaub *et al.* [5] conducted an elegant experiment under carefully controlled laboratory conditions. Bats were flown in a flight room containing two foraging compartments separated from each other by walls covered in sound-absorbing foam. Each compartment contained six landing platforms, two of which contained prey (live mealworms that produce similar rustling sounds to ground beetles). Each compartment also contained a speaker, and the bats were observed in the dark by using a video recorder and infrared illumination.

Four treatments were used in the experiments. The control was a playback of an empty sound file, and this served as a baseline for

measuring foraging activity in the absence of noise. Noise treatments were either continuous broadband noise, traffic noise played at levels equivalent to those experienced 10–15 m from a highway, or noise that mimicked the wind-induced movements of reeds along a river close to foraging areas used by greater mouse-eared bats. The noise treatments had a clear effect on how much time the bats spent searching for prey in the stimulus compartment: when traffic noise was broadcast, the bats spent 10% less time in the stimulus compartment compared with the silent control, and their prey capture rate also decreased by about 10%.

Even stronger effects were noted with playbacks of reed movement and broadband noise, even though the reed bed noise was 12 dB lower in amplitude than the traffic noise. The reed bed noise contained broadband clicks similar to those produced by arthropods moving in vegetation, and could be particularly effective at masking the sounds made by moving arthropods. Although acoustic masking seems to be the most likely explanation for reduced foraging activity and prey capture rates under noise, another factor may be the difficulties involved in processing multiple streams of auditory information simultaneously [10].

Anthropogenic noise has major consequences for hearing and signalling in animals. In future, it will be interesting to determine whether noise affects other taxa that rely on listening for prey-generated sounds, such as owls, in similar ways. It will be valuable to observe the foraging behaviour of bats that experience road traffic noise in nature, for example to determine if capture success deteriorates with distance from the road, and to determine if bats avoid road margins. Of course, roads also affect the behaviour of animals in other ways. Bats are sometimes killed by collisions with traffic [11]. Interestingly, street lights with mercury-vapour lamps attract aerial insects, and increase the densities of some aerial-feeding bat species [12].

Because aerial insects can be detected by echolocation, and the call frequencies of most echolocating bats are above the frequencies typically produced by traffic, it is



Figure 1. A greater mouse-eared bat searching for terrestrial prey. Photograph by Dietmar Nill.

unlikely that aerial feeding bats will be adversely affected by traffic noise. Extinction risk in bats is related to flight morphology, and species with short, broad wings (low aspect ratios) are especially vulnerable to extinction [13,14]. Many of these bats are gleaners that need manoeuvrable flight to find prey among vegetation, and which locate prey by listening for sounds produced by their movement — so the species most affected by noise are likely to be among those at greatest risk.

Increased urbanisation has resulted in fewer areas being devoid of roads. Today in the US, no area (other than in Alaska) is more than 35 km from a road and 6.3 million kilometres of roads cover the country [15]. Noise pollution has increased substantially in Europe in recent decades, and over 65% of inhabitants of the EU were exposed regularly to sound levels (55–65 dB) that led to serious annoyance, sleep disturbance and speech interference at the end of the last century [16]. Although the implications for human health are well documented [16], the consequences of noise pollution for conservation biology are often subtle and warrant further research. In particular, the effects of underwater noise pollution on marine mammals with well developed hearing may be severe. Low-frequency ambient marine noise levels have probably

increased by two orders of magnitude in the northern hemisphere over the last 60 years [17]. Male humpback whales increase song length if they hear low frequency (150–320 Hz) military sonar [18].

Evidence linking intense military sonar to strandings of beaked whales is compelling and suggests that the whales make sudden changes in dive trajectory whereupon they may die from the effects of decompression [19]. Catch rates of cod and haddock may be reduced by 50–70% following seismic surveys that use air guns to produce sound in the 20–150 Hz bandwidth [20]. A better understanding of the extent of noise pollution, and of its impact on animal sensory ecology in a range of environments is needed urgently.

#### References

1. Brumm, H., and Slabbekoorn, H. (2005). Acoustic communication in noise. *Adv. Stud. Behav.* 35, 151–209.
2. Brumm, H. (2004). The impact of environmental noise on song amplitude in a territorial bird. *J. Anim. Ecol.* 7, 434–440.
3. Brumm, H., Vos, K., Köllmer, I., and Todt, D. (2004). Acoustic communication in noise: regulation of call characteristics in a New World monkey. *J. Exp. Biol.* 207, 443–448.
4. Slabbekoorn, H., and den Boer-Visser, A. (2006). Cities change the songs of birds. *Curr. Biol.* 16, 2326–2331.
5. Schaub, A., Ostwald, J., and Siemers, B.M. (2008). Foraging bats avoid noise. *J. Exp. Biol.* 211, 3174–3180.
6. Arlettaz, R., Jones, G., and Racey, P.A. (2001). Effect of acoustic clutter on prey detection by bats. *Nature* 414, 742–745.
7. Russo, D., Jones, G., and Arlettaz, R. (2007). Echolocation and passive listening by foraging

- mouse-eared bats *Myotis myotis* and *M. blythii*. *J. Exp. Biol.* 210, 166–176.
8. Siemers, B.M., and Güttinger, R. (2006). Prey conspicuousness can explain apparent prey selectivity. *Curr. Biol.* 16, R157–R159.
  9. Goerlitz, H.R., Greif, S., and Siemers, B.M. (2008). Cues for acoustic detection of prey: insect rustling sounds and the influence of walking substrate. *J. Exp. Biol.* 211, 2799–2806.
  10. Barber, J.R., Razak, K.A., and Fuzessery, Z.M. (2003). Can two streams of auditory information be processed simultaneously? Evidence from the gleaner bat *Antrozous pallidus*. *J. Comp. Physiol.* 189A, 843–855.
  11. Russell, A.L., Butchkoski, C.M., Saidak, L., and McCracken, G.F. (2008). Road-killed bats, highway design, and the commuting ecology of bats. *Endang. Species Res.* DOI: 10.3354/esr00121.
  12. Rydell, J., and Racey, P.A. (1995). Street lamps and the feeding ecology of insectivorous bats. *Symp. Zool. Soc. Lond.* 67, 291–307.
  13. Jones, K.E., Purvis, A., and Gittleman, J.L. (2003). Biological correlates of extinction risk in bats. *Am. Nat.* 161, 601–614.
  14. Safi, K., and Kerth, G. (2004). A comparative analysis of specialization and extinction risk in temperate-zone bats. *Cons. Biol.* 18, 1293–1303.
  15. Watts, R.D., Compton, R.W., MacCammon, J.H., Rich, C.L., Wright, S.M., Owens, T., and Ouren, D.S. (2007). Roadless space of the conterminous United States. *Science* 316, 736–738.
  16. Dora, C. (1999). A different route to health: implications of transport policies. *Brit. Med. J.* 318, 1686–1689.
  17. International Whaling Commission Scientific Committee (IWC/SC). (2004). Annex K: Report of the Standing Working Group on Environmental Concerns. Annual IWC meeting, Sorrento, Italy, 29 June - 10 July 2004.
  18. Miller, P.J.O., Biasson, N., Samuels, A., and Tyack, P.L. (2000). Whale songs lengthen in response to sonar. *Nature* 405, 903.
  19. Jepson, P.D., Arbelo, M., Deaville, R., Patterson, I.A.P., Castro, P., Baker, J.R., Degollada, E., Ross, H.M., Herraes, P., Pocknell, A.M., et al. (2003) Gas-bubble lesions in stranded cetaceans. *Nature* 425, 575–576.
  20. Engås, A., Løkkeborg, S., Ona, E., and Soldal, A.V. (1996). Effects of seismic shooting on local abundance and catch rates of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). *Can. J. Fish. Aquat. Sci.* 53, 2238–2249.

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## Social Evolution: Daily Self-Sacrifice by Worker Ants

Each evening, a few workers of a Brazilian ant doom themselves to die overnight by remaining outside the nest to seal its entrance. This striking behaviour is a novel form of worker self-sacrifice.

Andrew F.G. Bourke

According to the precepts of Stalinist society exposed so vividly by Arthur Koestler in *Darkness at Noon*, the definition of an individual was “a multitude of one million divided by one million”. The implication is clear that, in such a society, selfhood has dissolved in a mass of interchangeable units, each existing only to serve the collective. This social model, nightmarish to the liberal human mind, is close to the reality in some insect colonies. In many species, workers have adaptations the use of which destroys or at least handicaps their bearer, while benefiting the colony. The canonical example is the sting of the honey bee worker, deployment of which kills the stinging bee [1]. In other cases, workers of some ants become distended and immobilized within the nest through use as living food stores [2], and larvae of other species provide queens with blood meals via special organs from which queens sip their haemolymph [3].

An international team of researchers, led by Adam Tofilski of the Agricultural University of Krakow and Francis Ratnieks of the University of Sussex,

has now added to the catalogue of adaptations for worker self-sacrifice by describing a novel behaviour in the Brazilian ant *Forelius pusillus* [4]. When external activity ends at the close of each day, a small group of workers seals the nest entrance from the outside with sand or soil. Because at night-time the external environment proves fatal to them, these workers effectively condemn themselves to death. This behaviour differs from previously-described forms of defensive self-sacrifice, like the stinging behaviour of honey bee workers, because it is not facultative: it does not arise in direct response to danger, but occurs routinely as a defence in anticipation of a possible threat. In the words of the researchers, it is pre-emptive self-sacrifice [4].

*Forelius* is a small genus of ants that occurs exclusively in the Americas and is typified by a fondness for nesting underground in hot, arid habitats [5]. One species, *F. pruinus* (formerly *Iridomyrmex pruinus*), is a desert and urban ant of the southern United States, foraging on the ground for small insect fragments and on vegetation for plant and homopteran secretions [6,7]. Colonies contain

multiple queens and up to 100,000 workers [6,7]. In general, however, little is known about the social and genetic structure of colonies of *Forelius* species. Tofilski et al. [4] studied a group of *F. pusillus* nests in bare sandy soil at the edge of a sugar cane field near São Simão, São Paulo State, Brazil. During the hot summer day, the tiny workers (each is around 2 mm long) labour for the colony by removing spoil from within the nest or by foraging. Excavation followed by dumping of the spoil creates a characteristic elliptical layer of spoil centred on the nest entrance. The researchers noticed that, towards sunset each evening, excavation and foraging ended and some workers began to seal the nest by placing sand and soil particles in the mouth of the entrance shaft. Nearly all workers returned inside before the nest was totally sealed, but, on almost every occasion, a few workers (one to eight) remained outside. These individuals walled themselves off from their nestmates by facing away from the nest entrance and kicking fine sand backwards (Figure 1) until the entrance was totally covered and barely distinguishable from its surroundings. The immediate reason for this was presumably that, given the sandy substrate, it achieved more effective closure and concealment than was possible from inside the nest.

In the morning, Tofilski et al. [4] found no workers near each nest entrance, which was always reopened from within by workers digging