## Current Biology **Dispatches**

- 3. López-Otín, C., Blasco, M.A., Partridge, L., Serrano, M., and Kroemer, G. (2013). The hallmarks of aging. Cell *153*, 1194–1217.
- Ezcurra, M., Benedetto, A., Sornda, T., Gilliat, A.F., Au, C., Zhang, Q., van Schelt, S., Petrache, A.L., Wang, H., de la Guardia, Y., et al. (2018). C. elegans eats its own intestine to make yolk leading to multiple senescent pathologies. Curr. Biol. 28, 2544–2556.
- Williams, G.C. (1957). Pleiotropy, natural selection, and the evolution of senescence. Evolution 11, 398–411.
- Blagosklonny, M.V. (2006). Aging and immortality: quasi-programmed senescence and its pharmacologic inhibition. Cell Cycle 5, 2087–2102.
- Hughes, S.E., Huang, C., and Kornfeld, K. (2011). Identification of mutations that delay somatic or reproductive aging of Caenorhabditis elegans. Genetics 189, 341–356.
- 8. Garigan, D., Hsu, A.L., Fraser, A.G., Kamath, R.S., Ahringer, J., and Kenyon, C. (2002). Genetic analysis of tissue aging in Caenorhabditis elegans: a role for heat-shock factor and bacterial proliferation. Genetics *161*, 1101–1112.
- 9. Herndon, L.A., Schmeissner, P.J., Dudaronek, J.M., Brown, P.A., Listner, K.M., Sakano, Y., Paupard, M.C., Hall, D.H., and Driscoll, M.

- (2002). Stochastic and genetic factors influence tissue-specific decline in ageing C. elegans. Nature *419*, 808–814.
- McGee, M.D., Weber, D., Day, N., Vitelli, C., Crippen, D., Herndon, L.A., Hall, D.H., and Melov, S. (2011). Loss of intestinal nuclei and intestinal integrity in aging C. elegans. Aging Cell 10. 699–710.
- de la Guardia, Y., Gilliat, A.F., Hellberg, J., Rennert, P., Cabreiro, F., and Gems, D. (2016). Run-on of germline apoptosis promotes gonad senescence in C. elegans. Oncotarget 7, 39082–39096.
- Palikaras, K., Mari, M., Petanidou, B., Pasparaki, A., Filippidis, G., and Tavernarakis, N. (2017). Ectopic fat deposition contributes to age-associated pathology in Caenorhabditis elegans. J. Lipid Res. 58, 72–80.
- Huang, C., Xiong, C., and Kornfeld, K. (2004). Measurements of age-related changes of physiological processes that predict lifespan of Caenorhabditis elegans. Proc. Natl. Acad. Sci. USA 101, 8084–8089.
- Rubinsztein, D.C., Mariño, G., and Kroemer, G. (2011). Autophagy and aging. Cell 146, 682–695.
- Gelino, S., Chang, J.T., Kumsta, C., She, X., Davis, A., Nguyen, C., Panowski, S., and Hansen, M. (2016). Intestinal autophagy improves healthspan and longevity in

- C. elegans during dietary restriction. PLoS Genet. *12*, e1006135.
- DePina, A.S., Iser, W.B., Park, S.S., Maudsley, S., Wilson, M.A., and Wolkow, C.A. (2011). Regulation of Caenorhabditis elegans vitellogenesis by DAF-2/IIS through separable transcriptional and posttranscriptional mechanisms. BMC Physiol. 11, 11.
- 17. Wang, H., Zhao, Y., Ezcurra, M., Benedetto, A., Gilliat, A.F., Hellberg, J., Ren, Z., Galimov, E.R., Athigapanich, T., Girstmair, J., et al. (2018). A parthenogenetic quasi-program causes teratoma-like tumors during aging in wild-type C. elegans. Aging Mech. Dis. 4, 6.
- McGee, M.D., Day, N., Graham, J., and Melov, S. (2012). cep-1/p53-dependent dysplastic pathology of the aging C. elegans gonad. Aging 4, 256–269.
- Hopkinson, J.M., Butte, N.F., Ellis, K., and Smith, E.O. (2000). Lactation delays postpartum bone mineral accretion and temporarily alters its regional distribution in women. J. Nutr. 130, 777–783.
- Carter, A.J., and Nguyen, A.Q. (2011). Antagonistic pleiotropy as a widespread mechanism for the maintenance of polymorphic disease alleles. BMC Med. Genet. 12, 160.

# **Animal Communication: Learning by Listening about Danger**

Christopher N. Templeton

Department of Biology, Pacific University, Forest Grove, Oregon, USA Correspondence: templeton@pacificu.edu https://doi.org/10.1016/j.cub.2018.07.039

A variety of animals eavesdrop and learn to use other species' alarm calls to avoid predators. Superb fairy-wrens, when hearing unfamiliar calls together with known alarm calls, can learn to associate these new calls with danger.

Hearing someone scream "Fire!" immediately conjures up a vision of bright orange flames, perhaps even a house or apartment building burning down. You might not have the same reaction to hearing "Dóiteáin", unless you happen to live in Galway, Ireland. But if you have a friend that speaks Gaelic, it might be useful to know that this means the exact same thing as "Fire!" before your own house burns down. Each animal species speaks a different 'language', yet it is not uncommon for animals to listen in on the vocal signals

of others. Eavesdropping between different species, 'heterospecifics', has been documented in many different species, from insects to whales. The majority of eavesdropping examples have focused on alarm calls and it isn't hard to imagine how knowing that a predator is nearby would be useful information for other species with similar ecologies and shared predators. There are dozens of examples of animals eavesdropping on heterospecific alarm calls [1], both across closely related (e.g., a songbird

eavesdropping on another songbird's alarm calls) and unrelated species (e.g., a songbird eavesdropping on a monkey's alarm calls). But how do animals actually know what the calls of other species mean? In a new paper in this issue of *Current Biology*, Dominique Potvin, Robert Magrath and colleagues [2] document for the first time an intriguing method by which an animal learns to recognize other species calls as alarm calls.

Alarm calls can transmit important information about predators [3–6]



#### **Current Biology Dispatches**

through signals indicating the type, even species of predator, and graded signals designating the degree of threat a predator poses, or some combination of these [7]. While alarm signals are designed to transmit information among individuals within a species (often to kin or social partners), they are also detectable by other species living in the same environment. Eavesdropping on the signals of other species has a clear advantage in that it dramatically increases the chances of obtaining social information about danger. Responding appropriately to another species' alarm signal requires first and foremost recognizing that a particular call is associated with danger and making this association requires learning.

Anti-predator signals are powerful stimuli for promoting learning; in fact 'teaching' young individuals which predators are dangerous was one of the first explanations for the function of mobbing calls [8]. This type of cultural transmission about predator identification is found in blackbirds (Turdus merula), which can learn to fear non-predatory birds (and even plastic bottles), by observing other individuals mobbing these non-threatening objects [9]. Likewise, after ground squirrels (Spermophilus lateralis) hear auditory playback of a novel sound and see a model hawk flying overhead, they increased their vigilance levels when they later hear the novel sound again, indicating that they had learned to associate it with danger [10]. Together, these studies demonstrate that animals can both learn about new predators from known alarm calls and learn about new alarm calls from known predators.

Now, Potvin and colleagues [2] build on this seminal work by examining the mechanisms through which superb fairy-wrens (Malurus cyaneus) learn to recognize new alarm calls. Fairy-wrens are brightly-colored Australian songbirds (Figure 1), perhaps most famous for their exceptionally high levels of extra-pair mating: 95% of nests contain offspring fathered outside the pair-bond, with more than 70% of all nestlings conceived outside of the pair [11]. Superb fairywrens also have an impressive alarm call system that includes mobbing calls [12]



Figure 1. Superb fairy wren. A male superb fairy-wren prepares to flee after hearing an alarm call. (Photo: Jessica McLachlan.)

used to recruit other individuals to harass predators or parasites and aerial alarm calls used to indicate the presence of a hunting raptor. Robert Magrath and colleagues have intensively studied the latter in fairy-wrens and other sympatric species [13-15], showing that these calls transmit information about predators to other fairy-wrens as well as other species living nearby. Similarly, fairywrens are known to flee to cover after hearing the alarm calls of a variety of other species. Because these species produce alarm calls with different acoustic structure and only fairy-wrens cooccurring with a species respond to that particular species' alarm calls, this reaction must be learned. How do they learn to associate these sounds with danger?

To address this question, Potvin and colleagues [2] conducted an elegant experiment (Figure 2): they paired a novel, non-threatening acoustic stimulus with a chorus of familiar alarm calls that a fairywren should already associate with danger. They observed that after this training, the new sound alone became associated with the apparent presence of a predator, causing receivers to flee in response to the formerly meaningless signal in much the same way that they would when hearing a more familiar alarm call. This learning by acoustic association takes place relatively rapidly (within 10–12

trials over 2-3 days) and lasts for at least a week after training. Perhaps most intriguingly, Potvin and colleagues [2] were able to train birds to respond to a novel alarm call in the absence of any actual predators, simply by pairing this novel call with familiar alarm calls. The idea that social learning might take place without visual reinforcement (actually seeing a predator) is particularly compelling because it suggests a novel mechanism for social learning: acoustic-acoustic association.

Social learning is commonly used by animals to obtain information about their environment and is a particularly useful strategy when it is difficult or costly to directly obtain information themselves [16]. Obtaining direct information about predators comes with obvious potential costs - risk of death - hence the importance of alarm calls as early warning systems. Yet, learning new alarm calls by associating the anti-predator behavior of prey with predators is also challenging: prey and predators often move quickly through dense habitats, making them difficult to detect visually. The acoustic-acoustic association documented by Potvin and colleagues [2] in fairy-wrens provides a useful way that animals can learn to associate new alarm calls with the presence of danger, even without having to observe the behavior of either the predator or prey.

### **Current Biology Dispatches**

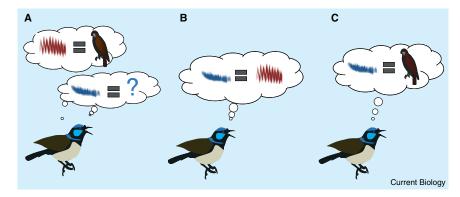


Figure 2. How birds use acoustic-acoustic association to socially learn about new alarm

(A) Fairy-wrens associate conspecific alarm calls (red) with predators, but do not initially respond to novel calls (blue). After training (B) using acoustic-acoustic association, fairy-wrens then associate the novel calls with predators (C).

Social learning by acoustic association has useful implications for conservation. Predator avoidance requires that prey recognize predators as threats and social learning can facilitate this process [17]. Learning about new predators is especially important when dealing with invasive predators that are often successful because their prey do not recognize them. For example, New Zealand robins (Petroica australis) do not recognize introduced stoats as threats. Training robins to recognize and respond to stoats has been a successful conservation strategy [18]. Would it be possible to use acoustic-acoustic social learning to train other species to associate robin alarm calls with stoats? Acoustic-acoustic association might also be useful for training captive-bred animals prior to release [17]. Training released animals to associate danger with the alarm calls of common species at the release site would facilitate avoidance of many different predators, without a need for training to recognize specific predators.

Moreover, the study of Potvin and colleagues [2] should inspire future research into the extent to which these social learning mechanisms are used by animals. For example, which type of signal lends itself to acoustic-acoustic social learning? It seems likely that the same principles described for high-threat alarm calls could also apply to mobbing signals, which are frequently eavesdropped on by heterospecifics. For example, nuthatches (Sitta canadensis)

eavesdrop on chickadee (Poecile atricapillus) mobbing calls [19], which vary depending on the threat level of the predator [20]. Could nuthatches use similar acoustic association mechanisms to learn not just that chickadee calls indicate danger but also to differentiate between more subtle variations of these calls? Could the same mechanism also be used to learn food calls or other types of vocalizations that animals use to communicate about other aspects of their environment? Are there constraints on which type of signals can be associated through this method? Are similar sounds or those with particular acoustic properties more readily learned? Investigating these and other questions about the mechanisms governing this new type of social learning should provide many opportunities for exciting future research.

#### REFERENCES

- 1. Magrath, R.D., Haff, T.M., Fallow, P.M., and Radford, A.N. (2015). Eavesdropping on heterospecific alarm calls: From mechanisms to consequences. Biol. Rev. 90, 560-586.
- 2. Potvin, D.A., Ratnayake, C.P., Radford, A.N., and Magrath, R.D. (2018). Birds learn socially to recognize heterospecific alarm calls by acoustic association. Curr. Biol. 28, 2632-2637
- 3. Crockford, C., Wittig, R.M., Mundry, R., and Zuberbühler, K. (2012). Wild chimpanzees inform ignorant group members of danger. Curr. Biol. 22, 142-146.
- 4. Suzuki, T.N. (2011). Parental alarm calls warn nestlings about different predatory threats. Curr. Biol. 21, R15-R16.

- 5. Griesser, M. (2009). Mobbing calls signal predator category in a kin group-living bird species. Proc. R. Soc. B. 276, 2887-2892.
- 6. Carlson, N.V., Healy, S.D., and Templeton, C.N. (2017). A comparative study of how British tits encode predator threat in their mobbing calls. Anim. Behav. 125, 77-92.
- 7. Hollen, L.I., and Radford, A.N. (2009). The development of alarm call behaviour in mammals and birds. Anim. Behav. 78, 791-800.
- 8. Curio, E. (1978). Adaptive significance of avian mobbing: 1. Teleonomic hypotheses and predictions. Zeit. Tierpsychol. 48, 175-183.
- 9 Curio F. Frnst U. and Vieth W. (1978). Cultural transmission of enemy recognition: one function of mobbing. Science 202, 899-901
- 10. Shriner, W.M. (1999). Antipredator responses to a previously neutral sound by free-living adult golden-mantled ground squirrels, Spermophilus lateralis (Sciuridae). Ethology . 105, 747–757.
- 11. Double, M., and Cockburn, A. (2000). Predawn infidelity: Females control extra-pair mating in superb fairy-wrens. Proc. R. Soc. B. 267, 465-470.
- 12. Feeney, W.E., Medina, I., Somveille, M., Heinsohn, R., Hall, M.L., Mulder, R.A., Stein, J.A., Kilner, R.M., and Langmore, N.E. (2013). Brood parasitism and the evolution of cooperative breeding in birds. Science 342, 1506-1508.
- 13. Magrath, R.D., Haff, T.M., McLachlan, J.R., and Igic, B. (2015). Wild birds learn to eavesdrop on heterospecific alarm calls. Curr. Biol. 25, 2047–2050.
- 14. Fallow, P.M., Pitcher, B.J., and Magrath, R.D. (2013). Alarming features: birds use specific acoustic properties to identify heterospecific alarm calls. Proc. R. Soc. B. 280, 20122539.
- 15. Magrath, R.D., and Bennett, T.H. (2012). A micro-geography of fear: learning to eavesdrop on alarm calls of neighbouring heterospecifics. Proc. R. Soc. B. 279, 902-909.
- 16. Galef, B.G., and Laland, K.N. (2005). Social learning in animals: Empirical studies and theoretical models. Bioscience 55, 489-499.
- 17. Griffin, A.S. (2004). Social learning about predators: A review and prospectus. Learn. Behav. 32, 131-140.
- 18. Maloney, R.F., and McLean, I.G. (1995). Historical and experimental learned predator recognition in free-living New Zealand robins. Anim. Behav. 50, 1193-1201.
- 19. Templeton, C.N., and Greene, E. (2007). Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. Proc. Natl. Acad. Sci. USA 104, 5479-5482.
- 20. Templeton, C.N., Greene, E., and Davis, K. (2005). Allometry of alarm calls: black-capped chickadees encode information about predator size. Science 308, 1934-1937.