11. Hoege, C., Constantinescu, A.T., Schwager, A., Goehring, N.W., Kumar, P., and Hyman, A.A. (2010). LGL can partition the cortex of one-cell Caenorhabditis elegans embryos into two domains. Curr. Biol. *20*, 1296–1303.
12. Tostevin, F., and Howard, M. (2008). Modeling the establishment of PAR protein polarity in the one-cell C. elegans embryo. Biophys. J. *95*, 4512–4522.
13. Munro, E., Nance, J., and Priess, J.R. (2004). Cortical flows powered by asymmetrical contraction transport PAR proteins to establish and maintain anterior-posterior polarity in the early C. elegans embryo. Dev. Cell *7*, 413–424.
14. Verkhovsky, A.B., Svitkina, T.M., and Borisy, G.G. (1999). Self-polarization and directional motility of cytoplasm. Curr. Biol. *9*, 11–20.

15. Yam, P.T., Wilson, C.A., Ji, L., Hebert, B., Barnhart, E.L., Dye, N.A., Wiseman, P.W., Danuser, G., and Theriot, J.A. (2007). Actin-myosin network reorganization breaks symmetry at the cell rear to spontaneously initiate polarized cell motility. J. Cell Biol. *178*, 1207–1221.
16. Mseka, T., Bamburg, J.R., and Cramer, L.P. (2007). ADF/cofilin family proteins control formation of oriented actin-filament bundles in the cell body to trigger fibroblast polarization. J Cell Sci. *120*, 4332–4344.
17. Mertens, A.E., Pegtel, D.M., and Collard, J.G. (2006). Tiam1 takes PARt in cell polarity. Trends Cell Biol. *16*, 308–316.
18. Wong, K., Van Keymeulen, A., and Bourne, H.R. (2007). PDZRhoGEF and myosin II localize RhoA activity to the back of polarizing neutrophil-like cells. J. Cell Biol. *179*, 1141–1148.

19. Machacek, M., Hodgson, L., Welch, C., Elliott, H., Pertz, O., Nalbant, P., Abel, L.A., Johnson, G.L., Hahn, K.M., and Danuser, G. (2009). Coordination of Rho GTPase activities during cell protrusion. Nature *461*, 99–103.
20. Slaughter, B.D., Smith, S.E., and Li, R. (2009). Symmetry breaking in the life cycle of the budding yeast. Cold Spring Harb. Perspect. Biol. *1*, a003384.

Ecole Polytechnique Fédérale de Lausanne, Laboratory of Cell Biophysics, Lausanne, 1015, Switzerland.
E-mail: alexander.verkhovsky@epfl.ch

# Sexual Signaling: Climatic Carry-Over

**A long term study of warblers in the Himalayas reveals a surprising contrast in the effects of warm springs as opposed to warm summers on a signaling trait, emphasizing the need to consider year-round influences of the environment on morphological variation.**

**Maren N. Vitousek\*, Roi Dor, and Rebecca J. Safran**

Sexual signals are widely used to convey information about their bearer to potential mates or competitors [1]. These signals are often condition-dependent, providing information about an individual's ability to withstand environmental challenges [2]. Current climate influences both condition and signal development, but until recently, little was known about whether signals reflected their bearer's ability to cope with prior environmental challenges [3,4]. Carry-over events — which occur in one season but influence success during subsequent seasons — have been demonstrated in a variety of species [5] and could have major influences on reproductive success in a rapidly changing climate. For example, when more of the non-breeding habitat of grey whales is covered by ice, females are in lower condition during the following breeding season, and produce fewer calves [6]. Such carry-over effects could be particularly influential for organisms that undertake large migrations and experience different environmental contexts along the way [7,8]. Examples include migratory songbirds whose plumage-based signals are typically developed in a non-breeding context,

often months before their use during territory acquisition and mate selection.

Several recent studies [3,4] using long-term data sets have begun to reveal links between prior environmental conditions and signal traits, with populations showing increased signal expression in years when non-breeding environmental conditions were favorable. In male barn swallows of the European subspecies (*Hirundo rustica rustica*), for instance, the length of sexually-selected tail streamers is increasing over time in association with climate-driven resource availability during migratory stop-overs [9]. As many aspects of the environment are expected to change rapidly in the near future, it will be increasingly important to understand potential interactions between multiple climate variables and signal traits. In a recent issue of *Current Biology,* Scordato *et al.* [10] use data collected over a 25 year period to show that warmer than average temperatures during different periods have opposing effects on the subsequent expression of a sexual signal — wing bar size – in the Hume's warbler (*Phylloscopus humei*).

Male Hume's warblers (Figure 1) with larger wing bars reproduce earlier, and males manipulated to display larger wing bars increase their territory size,

suggesting that this trait plays a role in male–male competitions during the breeding season [11]. The size of wing bars during the breeding season is determined by both the size of the trait during development, which occurs at the end of the breeding season and before long-distance migration, and the amount of wear during the non-breeding season. The surprising finding of Scordato *et al.* [10] is that the effect of increased temperature on wing bar size depends on the time during which temperature is elevated. When springs were warm, birds bred earlier, and early breeding was associated with the display of larger wing bars during the following breeding season. However, warm temperatures during the summer molt increased wear in the demelanized wing-bars. More worn bars had a smaller total bar area, suggesting that wing bar sizes were smaller in the breeding season following warmer summers. While spring and summer temperatures were not significantly correlated during the years of study, temperatures during both periods are increasing over time. Thus, an overall increase in breeding season temperatures due to climate shifts is expected to have contrasting influences on the size of the wing bar, a sexually selected trait.

**Signaling in a Changing Climate**
As global climate shifts, breeding dates are rapidly advancing in many bird species, driven by increasing spring temperatures [12]. Within populations, birds that arrive in better condition usually breed earlier, and early breeding itself confers a benefit to the individuals that are able to do so [13].

**Figure 1.** A male Hume's warbler (*Phylloscopus humei*) displays his wing bar.
Sexually selected wing bars are affected by climate variability in different ways depending on the time during which temperatures are elevated over the course of the year. Photo: Andrew Lassey.

However, as breeding dates advance, migration and breeding may no longer coincide with the periods of peak resource productivity, a phenomenon known as 'climate-change induced phenological mismatch' [14]. This mismatch between resource availability and demand may reduce survival and reproductive success when parents are forced to work harder to provide enough food for their offspring [15].

Scordato *et al.* [10] find that the breeding date of Hume's warblers has advanced by almost two weeks during the past twenty-five years, likely in response to a significant increase in mean spring temperature over the same period. But while early breeding predicted an increase in wing bar size in the following year, the mean wing bar size across populations had not increased over the study period [10]. These results suggest that while early breeding may confer benefits, the overall condition of individuals is unlikely to have improved over the study period. Despite the strong temporal effects of climate on wing bar size, which resulted in large fluctuations in the population's mean

wing bar size between years, variation in wing bar size across years varied little.

Strong climate effects on signal traits could erode their information content if signals are so strongly influenced by climate that they are no longer representative of the bearer's condition. Alternatively, climate shifts may not affect, or even reinforce the value of these traits as indicators of condition by increasing the cost of signal production and magnifying individual differences in condition. Determining whether signal traits remain reliable indicators of individual quality and reproductive success during periods of rapid environmental change is thus an important direction for future research.

**Dynamic Selection on Signal Traits**
Selection on signal traits is not constant, but fluctuates within and across populations [16]. Changes in the strength of sexual selection are driven at least in part by the effect of environmental variables on female mate selectivity and preferences [9,17–19]. Both traits and preferences can be plastic, although the degree of

plasticity and its heritability remain unclear [20]. Determining the relative role of plasticity in the development of signal traits that influence reproductive success is also vital for understanding how climate fluctuations will influence sexual signaling. Scordato *et al.* [10] report that mean adult wing-bar size was correlated with mean chick wing-bar size across years, which could result from heritability, parental investment, or both. Estimates of heritability of wing bar size in Hume's warblers were low to moderate, and surprisingly, there was no evidence of maternal (or paternal) effects acting on this trait [10]. Thus, the authors conclude that large between-year changes in trait size are driven more by phenotypic plasticity than by viability selection. The potential role of fluctuations in mate selection for signal traits has yet to be determined, but appears unlikely to generate the strong inter-annual trait variability detailed here.

The emerging picture suggests that both traits and preferences are plastic and dynamic, reflecting an individual's condition and its influence by past and present environments. As demonstrated by Scordato *et al.* [10] the effect of environmental factors may be complex, with climate variables exerting opposite effects on signal elaboration depending on the life history stage in which they occur. Understanding these dynamic links between genetic determination, environment, signal expression, and mate selection will help to reveal how signals convey information about their bearer across changing environmental contexts.

**References**
1. Andersson, M.A. (1994). Sexual Selection (Princeton: Princeton University Press).
2. Hill, G.E. (2011). Condition-dependent traits as signals of the functionality of vital cellular processes. Ecol. Lett. *14*, 625–634.
3. Saino, N., Szép, T., Romano, M., Rubolini, D., Spina, F., and Møller, A.P. (2004). Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. Ecol. Lett. *7*, 21–25.
4. Hegyi, G., Török, J., Garamszegi, L.Z., Rosivall, B., Szöllősi, E., and Hargitai, R. (2007). Dynamics of multiple sexual signals in relation to climatic conditions. Evol. Ecol. Res. *9*, 905–920.
5. Harrison, X.A., Blount, J.D., Inger, R., Norris, D.R., and Bearhop, S. (2011). Carry-over effects as drivers of fitness differences in animals. J. Anim. Ecol. *80*, 4–18.
6. Perryman, W.L., Donahue, M.A., Perkins, P.C., and Reilly, S.B. (2002). Grey whale calf production in 1994-2000: are observed fluctuations related to changes in seasonal ice cover? Marine Mammal Sci. *18*, 121–144.

7. Norris, D.R., Marra, P.P., Kyser, T.K., Sherry, T.W., and Ratcliffe, L.M. (2004). Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proc. R. Soc. B 271, 59–64.

8. Reudink, M.W., Marra, P.P., Kyser, T.K., Boag, P.T., Langin, K.M., and Ratcliffe, L.M. (2009). Non-breeding season events influence sexual selection in a long-distance migratory bird. Proc. R. Soc. B 276, 1619–1626.

9. Møller, A.P., and Szép, T. (2005). Rapid evolutionary change in a secondary sexual character linked to climatic change. J. Evol. Biol. 18, 481–495.

10. Scordato, E.S.C., Bontrager, A.L., and Price, T.D. (2012). Cross-generational effects of climate change on expression of a sexually selected trait. Curr. Biol. 22, 78–82.

11. Marchetti, K. (1998). The evolution of multiple male traits in the yellow-browed leaf warbler. Anim. Behav. 55, 361–376.

12. Both, C., Artemyev, A.V., Blaauw, B., Cowie, R.J., Dekhuijzen, A.J., Eeva, T., Enemar, A., Gustafsson, L., Ivankina, E.V.,

Järvinen, A., et al. (2004). Large-scale geographic variation confirms that climate change causes birds to lay earlier. Proc. R. Soc. Lond. B 271, 1657–1662.

13. Verhulst, S., and Nilsson, J.-A. (2008). The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. Phil. Trans. R. Soc. B 363, 399–410.

14. Visser, M.E., Both, C., and Lambrechts, M.M. (2004). Global climate change leads to mistimed avian reproduction. Adv. Ecol. Res. 35, 89–110.

15. Thomas, D.W., Blondel, J., Perret, P., Lambrechts, M.M., and Speakman, J.R. (2001). Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. Science 291, 2598–2600.

16. Chaine, A.S., and Lyon, B.E. (2008). Adaptive plasticity in female mate choice dampens sexual selection on male ornaments in the lark bunting. Science 319, 459–462.

17. Cockburn, A., Osmond, H.L., and Double, M.C. (2008). Swingin' in the rain: condition dependence and sexual selection in

a capricious world. Proc. R. Soc. B 275, 605–612.

18. Slagsvold, T., Lifjeld, J.T., Stenmark, G., and Breiehagen, T. (1988). On the cost of searching for a mate in female pied flycatchers Ficedula hypoleuca. Anim. Behav. 36, 433–442.

19. Vitousek, M.N. (2009). Investment in mate choice depends on resource availability in female Galapagos marine iguanas (Amblyrhynchus cristatus). Behav. Ecol. Sociobiol. 64, 105–115.

20. Nussey, D.H., Postma, E., Gienapp, P., and Visser, M.E. (2005). Selection on heritable phenotypic plasticity in a wild bird population. Science 310, 304–306.

Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, 80309, USA.
*E-mail: maren.vitousek@colorado.edu

# Developmental Biology: Taking Flight

**Powered flight was first mastered by insects, many millions of years ago. Now, studies with the fruit fly Drosophila melanogaster reveal the critical role of a conserved transcription factor in programming the development of specialized flight muscles.**

**Sudipto Roy[1] and K. VijayRaghavan[2]**

*"God in his wisdom made the fly, And then forgot to tell us why."* It must have been an annoying buzzing that brought Ogden Nash to pen his famous poem. But the flight manoeuvres of insects, and in particular flies, are also sophisticated: they hover; rapidly change direction, dive and even fly backwards. Anatomically, insect flight probably first evolved by muscles inserting into the wing hinge: mayflies and dragonflies are extant examples where flight is powered by such 'direct' flight muscles. In most insects, however, flight is powered by controlling wing oscillation differently, namely through indirect flight muscles (Figure 1A). They are called 'indirect' because the muscles insert into the thoracic exoskeleton and produce high frequency wing vibrations by inducing cyclic deformations of the thoracic cuticle and of the wings as an indirect consequence.

Indirect flight muscles also have an unusual physiology: the contraction of one set of muscles stretches another, which in turn causes contraction and stretching of the first set. This results in an oscillation of the thoracic box. The motor neuron's role is to stimulate the muscle periodically, causing the release of $Ca^{2+}$ ions in the muscle, necessary to sustain contraction. The motor neuron firing frequency is asynchronous with indirect flight muscle contraction: the latter can be at several hundred to a 1000 Hz, while the former is usually tens of Hz (Figure 1C). Indirect flight muscles are thus stretch-activated and asynchronous, as distinct from other muscles such as those of the insect leg, which are activated by synchronous neuronal firing. The unusual physiology of the indirect flight muscles is made possible by their specialized structure in which the muscles are arranged in unaligned fibre bundles, hence the term 'fibrillar muscle', with the endoplasmic reticulum (ER) in the periphery. In contrast, other muscles, such as those of the insect leg, have a more distributed ER and myofibres aligned in a 'tubular' form [1]. While the physiology, ultrastructure and development of indirect flight muscles have been extensively investigated [2,3], the mechanism by which the fibrillar fate is instituted had remained unclear. In a recent paper, Schnorrer

and co-authors [4] report that, in Drosophila, Spalt major (Salm), a zinc finger transcription factor, functions as a 'master regulator' driving muscle progenitors to differentiate into indirect flight muscles.

An earlier indication for a role of the salm gene in indirect flight muscle formation came from a study that screened for genes regulating muscle development in Drosophila [5]. The new work [4] now suggests that Salm is a molecular switch that programs the distinctive properties of the indirect flight muscles. Flies deprived of salm function in muscle precursors form fewer and abnormal indirect flight muscles whose myofibrillar organization is shifted from fibrillar to tubular. The effect of salm was specific for the indirect flight muscles, and the formation and function of the tubular muscles, such as those in the leg, remained unaffected.

In Drosophila, embryonic muscle precursors first assemble a set of body wall muscles that allow the larvae to crawl around. Then, during metamorphosis, larval muscles degenerate, and adult muscle precursors fuse and differentiate into new sets of muscles engineered for walking and flight [3]. Indirect flight muscles develop through a precisely choreographed series of events [2,3,6]. The development of one set of indirect flight muscles, the dorsal longitudinal muscles, is rather peculiar in that the adult muscle precursors fuse with three larval muscles that escape