cognition then why not also to other domesticated and self-domesticated species? Hare and Woods point to self-control. Self-control, or ‘inhibition’, seems to come alongside having large brains. Early *Homo sapiens* had large brains but so did other early human species. Where the dogs and bonobos have (self)domestication without much self-control, other early human species likely had self-control without self-domestication. Hare and Woods propose that *Homo sapiens* had both traits, and this is what gave us an edge over other early human species. They dive more into the genetics of it, giving a clear and detailed explanation (to a non-expert, such as myself) on the roles of ‘librarian genes’ that can control how each gene is read. Librarian genes that control neural crest cell development are a candidate for self-domestication, with modified neural crests found in domesticated species and also differing at the split between us and other human species. The authors build up a very cohesive and compelling theory on the role of friendliness in human evolution. And then they get political.

From Chapter 6 onwards, Hare and Woods outline how selection for friendliness may also have given rise to dehumanisation and go on to centre all the world’s problems on this hypothesis. They begin with a brief history of migration, colonialism and conflict in the border regions of the Democratic Republic of the Congo, Rwanda, Burundi, Uganda and Tanzania, told through the personal history of their nanny. They use this as a backdrop against which to talk about how the self-domestication hypothesis, with its changes in the oxytocin system, predicts not only increased friendliness but also an ability to dehumanise and aggressively punish those in ‘out-groups’. They discuss ‘simianization’ (comparing people to apes or monkeys) as a common form of dehumanisation. They propose that contact with people from different groups is the best way for us to learn not to dehumanise them, and that urban architecture can promote communities by designing cities that bring us together. Finally, they talk about how kindness to animals can be related to kindness to other people, and they end with the sentiment that “our lives should be measured not by how many enemies we have conquered, but by how many friends we have made. That is the secret to our survival.”

I have rushed through the summaries of these last chapters a little because there are kernels within them in which I can see the value. It is absolutely necessary that we learn how to stop dehumanising one another, and I really enjoy thinking about how to build inclusive communities. I can see that “being friendlier to others” is a really appealing solution for us as individuals. But where the first five chapters showed a deep familiarity with great ape and canine cognitive research within psychology, the final four chapters showed a real reticence to move beyond a psychological perspective. When the social sciences were mentioned here, the concepts were cherry-picked and presented in a way that suggested that there is a disparate scattering of views on racism in America (not to mention the rest of the world). In fact, the social sciences present a very strong framework for understanding structural inequalities, and I would have loved to see the authors fold their own hypothesis into this structural narrative. Psychological hypotheses around ‘human nature’ often fail to situate themselves within a broader societal analysis. The field of psychology seriously needs to enter into a sincere discourse with social sciences, so that we can work towards a fuller understanding of the interplay between individual minds and the societies in which these minds exist. We live in a system of global racial capitalism. While we all work on being friendlier to one another, we need to be dismantling this system as well.

REFERENCES

1. MacLean, E.L., Herrmann, E., Suchindran, S., and Hare, B. (2017). Individual differences in cooperative communicative skills are more similar between dogs and humans than chimpanzees. Anim. Behav. *126*, 41–51.
2. Hare, B., Plyusnina, I., Ignacio, N., Schepina, O., Stepika, A., Wrangham, R., and Trut, L. (2005). Social cognitive evolution in captive foxes is a correlated by-product of experimental domestication. Curr. Biol. *15*, 226–230.
3. Tan, J., and Hare, B. (2013). Bonobos share with strangers. PLoS One *8*, e51922.

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Quick guide

Hybrid zones

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What are hybrid zones and why are they interesting? Hybrid zones are regions in which distinct populations of organisms meet, mate and produce genetically admixed — hybrid — offspring (Figure 1). Typically, the fitness of hybrid offspring is lower than that of the parents, because the diverged genomes derived from the two parental populations may have difficulty functioning together in a hybrid individual. Actually, such genetic incompatibilities between the parental genomes are exposed in the hybrid zone. Hence, hybrid zones provide insight into the genetic barriers that underlie the origin of species.

Wait… aren’t individuals that hybridize part of the same species? It depends. If the parental populations manage to maintain their overall genomic integrity in the face of hybridization, this confirms that reproductive isolation has evolved between them. Otherwise the populations would fuse and the hybrid zone would cease to exist. Therefore, a hybrid zone that is maintained over time reflects a limitation to gene flow between the populations involved. Such an enduring hybrid zone could be considered to provide support for species status, rather than pose an argument against it. In fact, the distribution ranges of many recognized species meet at hybrid zones.

How do hybrid zones come to be? Hybrid zones typically originate when two closely related but geographically isolated populations expand their respective ranges towards each other and come into contact. This requires the following conditions. The populations involved initially arose because range fragmentation, for example during an ice age’s cold spell, partitioned a formerly continuous ancestral population. This isolation initiated independent evolution of the daughter populations. As a by-product, their genetic compatibility gradually decreased. When secondary contact between the daughter populations is regained, say during an ice age’s warm spell, any reproductive isolating mechanism that evolved is

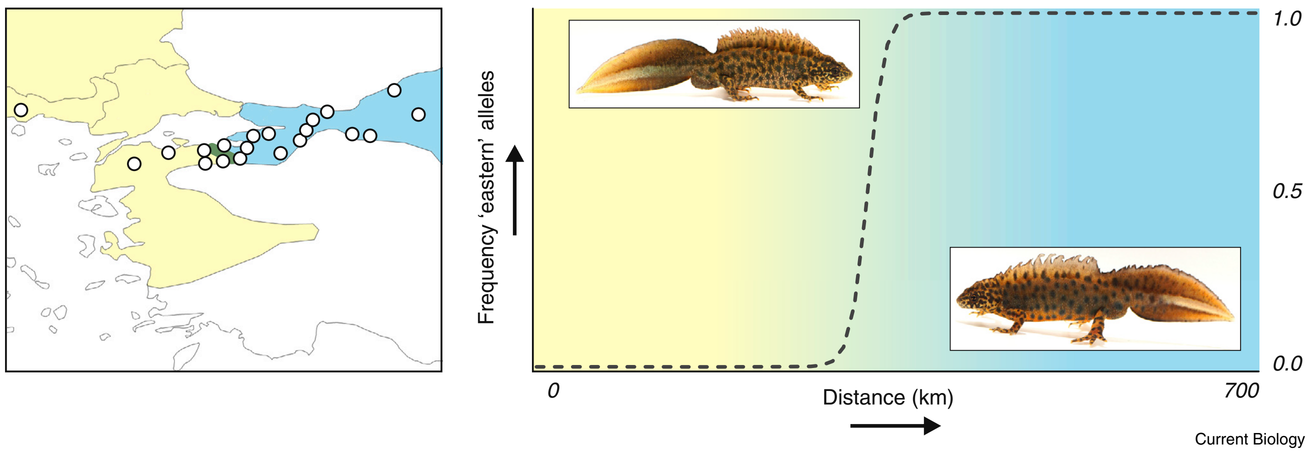

Figure 1. An example of a hybrid zone from crested newts in Turkey.
Newt populations (the dots on the map) are sampled along a transect that runs from the species *Triturus ivanbureschi* in the west (yellow) to the species *T. anatolicus* in the east (blue). The graph depicts the proportion of alleles diagnostic for the eastern species. Hence, a value of 0 corresponds to the western species and a value of 1 to the eastern species. Intermediate frequencies are observed in the hybrid zone (in green on the map; photos: Michael Fahrbach.).

put to the test. If hybrids are produced, but their fitness is lower than pure-bred individuals, a hybrid zone will form. Most hybrid zones observed today were established after species expanded their ranges during the current interglacial period, such as the famous hybrid zone between two species of fire-bellied toad in Europe.

Can genes flow through a hybrid zone? If hybrid offspring are not completely sterile, this means they can backcross with members of the parental populations. Backcrossing provides an opportunity for gene copies (alleles) that evolved in one population to flow, through the hybrid zone, into the other population. This process is known as introgression. Natural selection inhibits the transfer of alleles that perform worse in the other population but would drag advantageous alleles into the receiving population. Alleles without a particular disadvantage or benefit may introgress by chance. Genetic studies have revealed introgression across hybrid zones to be the rule rather than the exception (sometimes covering hundreds of kilometers, as in crested newts in Europe and adjacent Asia). So, while hybrid zones allow the parental populations to maintain their overall genetic integrity, they also mediate genetic exchange between them.

What determines the position of a hybrid zone? The width of hybrid zone is determined by a balance between negative selection against hybrids and the influx of pure parentals (Figure 1). There are two main models that aim to explain where on the landscape a hybrid zone settles. The tension zone model suggests that endogenous (intrinsic) selection, in the guise of hybrid breakdown, regulates the hybrid zone and incites the zone to come to rest where population density is relatively low. By contrast, the geographical selection-gradient model suggests that exogenous (environment-dependent) selection maintains the position of the hybrid zone, because the two parental populations involved are favoured on either side of the zone. These two models are not mutually exclusive and both would predict that hybrid zones tend to settle at ecological transitions (ecotones).

Can hybrid zones move? Hybrid zones were traditionally thought to be quite stable. Yet, it is unlikely that two hybridizing populations have equal fitness, where the hybrid zone between them initially formed. The population that has a competitive edge could outcompete and replace the other one, until they reach an equilibrium position where both have equal fitness. In the process, the hybrid zone would shift across the landscape. It is unclear how often and how far hybrid zones move. Some zones are thought to have been stable since their origin. However, movement has been observed 'live' over decades (e.g. chickadees in North-America), or has been inferred from a genetic footprint of introgressed alleles (e.g. the aforementioned crested newts).

Can hybrid zones inform us about climate change? Just like hybrid zones can provide insight into past distribution dynamics, they can be used to make predictions about future range rearrangements, too. Global warming basically changes the location of an ecotone. In response, a hybrid zone may track this ecotone. Therefore, hybrid zones that are monitored over time (such as the chickadees mentioned above) can potentially be used as a marker for global warming: the movement of a hybrid zone, across a continent or along an elevational gradient, can teach us how species respond to contemporary climate change.

Where can I find out more?

Barton, N.H., and Hewitt, G.M. (1989). Adaptation, speciation and hybrid zones. Nature *341*, 497–503.
Endler, J.A. (1977). Geographic Variation, Speciation, and Clines (Princeton University Press).
Harrison, R.G., and Larson, E. (2014). Hybridization, introgression, and the nature of species boundaries. J. Hered. *105*, 795–809.
Taylor, S.A., Larson, E.L., and Harrison, R.G. (2015). Hybrid zones: windows on climate change. Trends Ecol. Evol. *30*, 398–406.
Wielstra, B. (2019). Historical hybrid zone movement: more pervasive than appreciated. J. Biogeogr. *46*, 1300–1305.

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