BEHAVIOR

Local convergence of behavior across species

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Behavior is a way for organisms to respond flexibly to the environmental conditions they encounter. Our own species exhibits large behavioral flexibility and occurs in all terrestrial habitats, sharing these environments with many other species. It remains unclear to what extent a shared environment constrains behavior and whether these constraints apply similarly across species. Here, we show that foraging human populations and nonhuman mammal and bird species that live in a given environment exhibit high levels of similarity in their foraging, reproductive, and social behaviors. Our findings suggest that local conditions may select for similar behaviors in both humans and nonhuman animals.

Wherever they live, animals display diverse behaviors to cope with the many challenges they face—from foraging for food to finding shelter and protection to meeting with mates for reproduction (*1*). In any particular environment, a diversity of behavioral solutions might be expected given the differences in how animals experience and exploit their environment, especially if species fill specific niches to reduce resource competition (*2*). At the same time, local ecological constraints might only permit a certain range of behaviors. In this case, species with similar behaviors would be expected to assemble in a given environment. Convergence of behavior to ecological conditions has been found among closely related species (*3*–*5*), and consistent influences of ecological conditions on evolutionary patterns across distantly related taxonomic groups have been described for morphology [e.g., Bergman's rule (*6*) or Allen's rule (*7*)] and life history (*8*). On the basis of this interplay of competition and adaptation, we predict that a limited subset of behaviors will exist at each locality, with similar behaviors found in similar environments around the world.

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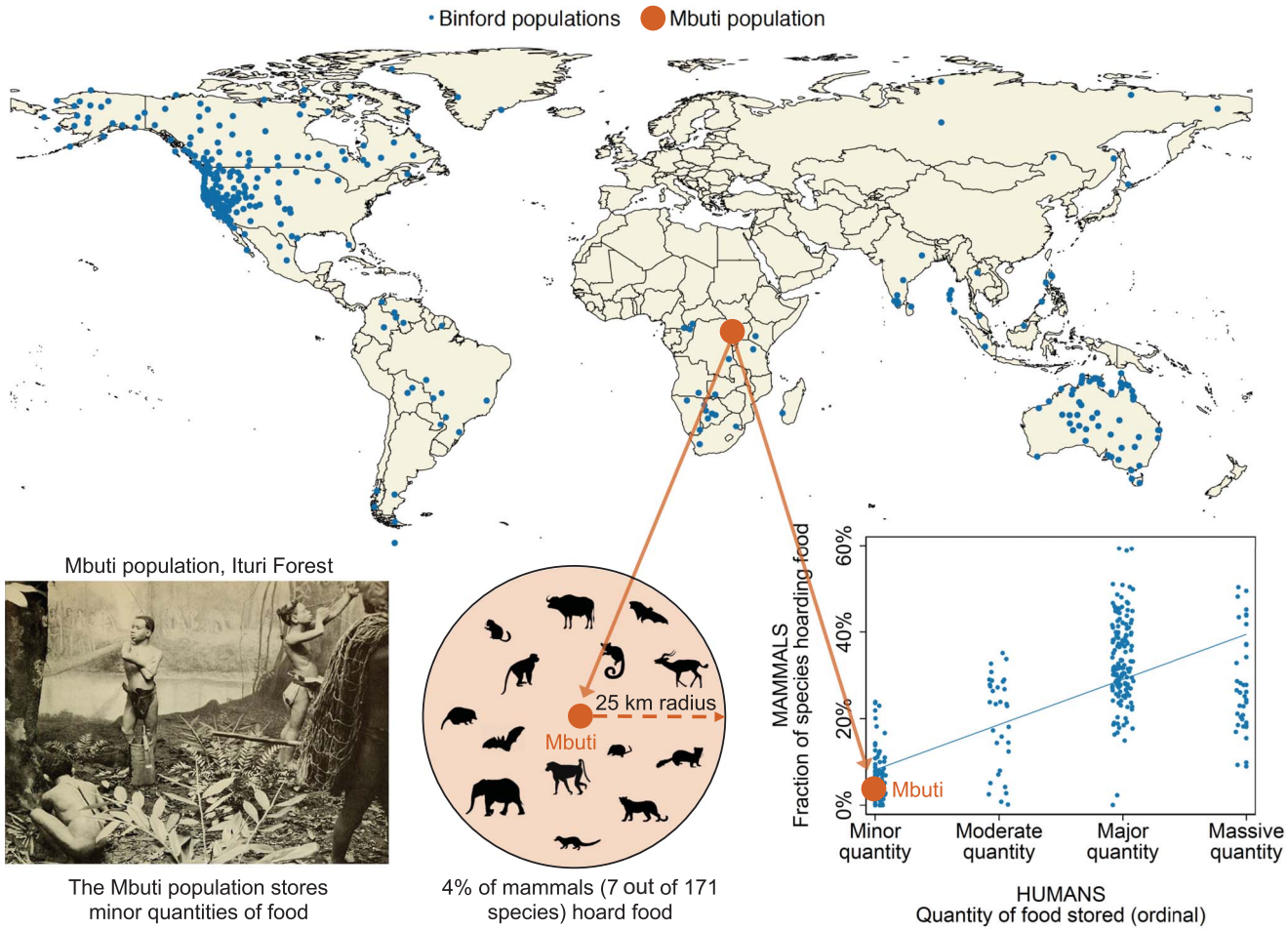

Fig. 1. Matching the behavioral variation of foraging humans, mammals, and birds around the world. For each of the 339 small-scale, subsistence-foraging populations from around the world (dots on map), we determined which mammal and bird species lived in the same location and computed their average behavior. For example, in the Mbuti population, which lives in the African rainforests, food storage is only minor and only 4% of the 171 mammal species living within a 25-km radius around the center of their population hoard food. Combining this information across populations shows that generally in locations where food storage among humans is more common, a higher proportion of local mammal species hoard food, as indicated by the upward slope in the scatter plot. Photo credit: Flickr Commons/PhyloPic public domain.

The role of ecological conditions in constraining behavioral variation is particularly debated with regards to our own species, which has colonized essentially all terrestrial environments in the world. On the one hand, there is evidence that cultural processes are responsible for the large variation in behavior observed across societies (*9*) and that we humans build our own ecological niche (*10*). By influencing the local ecology, humans might also make it more difficult for species with similar behaviors to coexist (*11*). Alternatively, human behavioral ecology contends that even if behavioral variation among societies primarily originates through cultural processes, the ecological constraints that influence behavior in other species also generally apply to our own species (*12*–*14*). We predict an interplay of competition and adaptation for humans, too: Different human societies might acquire different behaviors through different paths, but specific behaviors will be present where they fit into the local environment (*15*–*18*).

In this work, we take a unifying perspective and scrutinize the central tenet of behavioral ecology—that there are consistent and predictable adaptations to ecological conditions, which potentially operate across very different taxonomic groups. Specifically, we study whether the foraging, reproductive, and social behaviors of humans, mammals (we use the term mammal to refer to all species in the class Mammalia excluding humans), and birds are more similar to the behaviors of other species found in the same environment than they are to the behaviors found in different environments.

We built our analysis around an ethnographic database that provides data on the behavior of 339 human hunter-gatherer populations from around the world (*19*). Our focus is on small-scale, subsistence-foraging human populations because these populations are generally tied to a specific location. Additionally, their reliance on acquiring food from the available local resources means that we are more likely to detect ecological influences on their behavior, should they exist (*20*). For each of the human populations, we first identified all mammal and bird species that live in the same location. We then identified 15 behavioral variables encoded in the human database (six foraging, five reproductive, and four social behaviors) for which closely comparative data existed for the nonhuman species (tables S1 to S3). We assigned the typically observed behavior to each species (because both the extent and availability of data on behavioral variation within other species is limited) and computed average mammal and bird behaviors at the

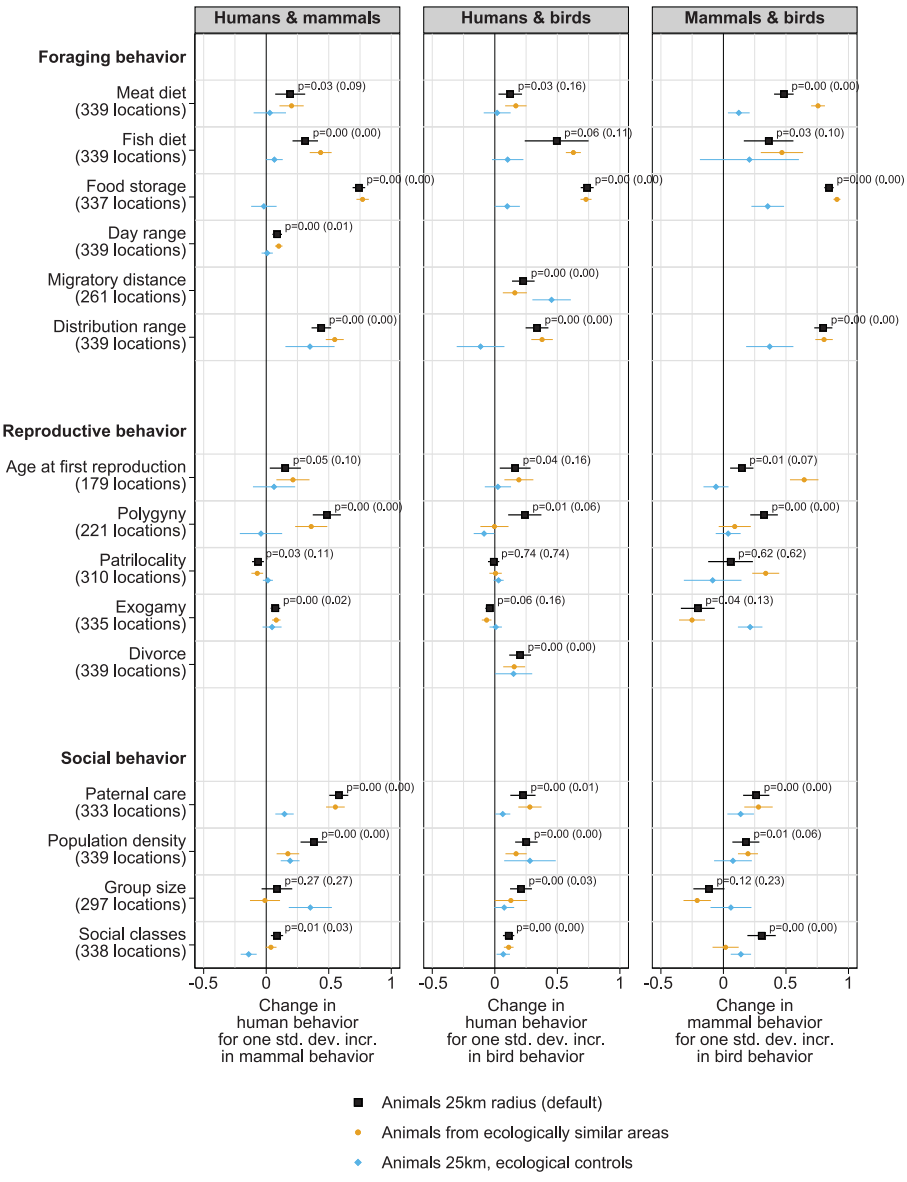

Fig. 2. Association in behavior between humans, mammals, and birds living at the same location. Dots show the estimated marginal effect of an ordinary least squares (OLS) regression and lines show the 90% confidence intervals. For the main specification, the figure also provides the unadjusted *P* values and *P* values that are adjusted for multiple testing in parentheses. All variables are standardized with a mean of 0 and a standard deviation (SD) of 1. The marginal effect thus shows by how many SDs human behavior changes for a 1-SD increase (std. dev. incr.) in mammal behavior (column 1), by how many SDs human behavior changes for a 1-SD increase in bird behavior (column 2), and by how many SDs mammal behavior changes for a 1-SD increase in bird behavior (column 3). For binary outcomes, the marginal effect reflects the change in the likelihood of a positive outcome for a 1-SD increase in mammal or bird behavior. We present estimates from three different specifications: (i) average behavior of all nonhuman species found within a 25-km radius of the center of the range of human populations (main specification), (ii) average behavior of nonhuman species in ecologically similar areas, and (iii) same as (i) but additionally controlling for ecological conditions.

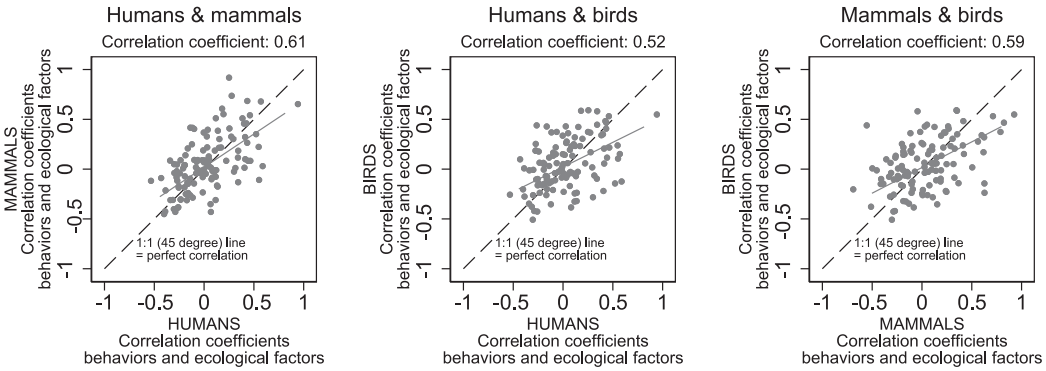

Fig. 3. Similarity in the correlation between behaviors and ecological factors across humans, mammals, and birds living at the same location. These plots visualize the similarity in correlation coefficients between different behaviors and ecological factors for humans, mammals, and birds. They reflect correlations between all 12 behaviors that we observe for the three groups and 10 ecological variables (including main biomes, in which Binford populations are located, latitude, altitude, and proximity to coast). See fig. S11 for more details on the underlying correlations.

different locations. We were thus able to analyze the association between human, mammal, and bird behaviors across locations (Fig. 1).

Our results show that foraging human populations, mammals, and bird species that share a local environment converge in their foraging, reproductive, and social behaviors (Fig. 2). Specifically for foraging behavior (see also fig. S5), we detected the following: (i) Human populations that rely more on hunting terrestrial vertebrates for food occur where a higher proportion of local mammals and birds rely on vertebrates. (ii) Human populations that rely more on aquatic organisms for food occur where a higher proportion of local mammals and birds eat fish. (iii) We observed associations between the reliance of humans on food storage and the proportion of local mammals and birds that hoard food. (iv) There were associations in short-term movements to acquire resources, with human populations being central-place foragers (which is usually associated with longer day ranges because of local resource depletion) in locations where mammals have longer daily foraging trips (no bird data available). (v) There were also associations in long-term movements between resource locations, with humans moving longer distances between foraging locations in environments where birds migrate longer distances (no mammal data available). (vi) We observed associations between the total distribution area occupied by a human population and that occupied by the local mammal and bird species.

For reproductive behavior (see also fig. S6), we found the following connections in behavior: (i) Global variation in the age of first reproduction is linked across humans, mammals, and birds. (ii) Males are more likely to monopolize matings in certain places, with a higher proportion of human men being married to multiple women, more mammals living in unstable groups [providing monopolization potential (*21*)], and male birds investing more into their plumage to attract multiple females. (iii) In those locations where humans marry outside their group, mammals show longer breeding dispersal movements but birds show shorter ones. (iv) Splits between mating partners are more likely in some areas, with divorce permitted in human populations and bird pairs more likely to split up each year. (v) We did not find consistent associations between humans, mammals, and birds for patrilocality, where males stay at and females move away from their place of birth.

For social behavior (see also fig. S7), our analyses revealed the following associations: (i) The relative role of fathers contributing resources to offspring differed—in locations in which human males provide a higher proportion of the diet for their family, males contribute to the feeding and carrying of offspring in a higher proportion of mammal species and are the sole providers of parental care in a higher proportion of bird species. (ii) Where humans live in higher densities, so do other mammals and birds. (iii) In locations in which residential group sizes in humans are larger, social group sizes of mammals are larger and birds are more likely to forage in groups than to rely on solitary foraging. (iv) Where human populations have social classes, more mammals and birds have a social system with dominant breeders and subordinate nonbreeding helpers.

Similarities in the behaviors of humans, mammals, and birds appear to result from selection pressures of the local environment. First, associations across species decline when we include ecological variables as covariates to explain the variation in behaviors (including biomes, latitude, altitude, and proximity to coast) (Fig. 2 shows results with ecological controls), which is consistent with the argument that ecological conditions constrain behavior. Second, associations between the same ecological variables and behaviors are very similar across humans, mammals, and birds (Fig. 3). Third, human behavior from one location matches that of animals found at another location with similar ecological characteristics (Fig. 2 shows results for animals from ecologically similar areas), which corroborates the hypothesis that associations arise from a consistent influence of ecological factors rather than spatial autocorrelation. Local convergence of behavior across species occurs in all environments, and the associations are not the result of extreme behaviors in extreme environments [fig. S2 shows results with controls for coastal and (sub)arctic areas]. In line with this evidence, although the associations in behavior across species are strongest when tested in the large worldwide sample, most associations are also present on a smaller scale when tested in an independent dataset of human populations in North America (fig. S4). Our results recapture several of the previously described associations between specific ecological factors and individual human (*22*, *23*) or nonhuman behaviors (*3*–*5*), which suggests that combining findings from different taxonomic groups might lead to a deeper understanding of how ecology shapes behavior.

Overall, our results highlight that environmental conditions appear to constrain the behaviors of humans and other animals in similar ways. Although our findings cannot reveal the processes of adaptation and how ecology interacts with cultural transmission processes that shape behavior, they suggest that there generally tends to be a specific set of behavioral solutions to the environmental challenges at a given location that is shared by humans, mammals, and birds. This pervasive influence of ecology on behavior raises the question of whether the behavioral diversity of modern human populations still reflects local ecological conditions, even though agriculture, market integration, and technology might modulate the response of behavior to local conditions.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Text
Figs. S1 to S11
Tables S1 to S7
References (*25*–*71*)

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