even be maintained in the face of parasitic interactions. For example, the caterpillars of at least three species of Masacinae (Table 1) live inside Myrmica ant nests to feed on the larval brood of their host ant species (22). Hence, this study points to the possibility that under selection for symbiotic associations, the calls of one insect species have evolved to attract other, distantly related insect species.

REFERENCES AND NOTES

7. The third to fifth (and final) instar caterpillars of Thibon ventralis bear the three distinct sets of specialized organs for associating with ants: (i) paired, eversible organs which secrete food to ants on segment A-8; (ii) paired, eversible organs that presumably secrete a substance to ants on segment T-3; and (iii) a pair of chitinized vibratory papillae on the anterior edge of segment T-1 that, in concert with oscillating the head in and out, beat most frequently when caterpillars are walking or are stressed. First and second instar caterpillars possess none of these organs. For a detailed account of T. ventralis caterpillar biology see DeVries (4).
8. Calls were detected by placing caterpillars on a taut paper membrane sandwiched between 4-inch diameter plastic rings that had a particle velocity microphone touching the paper membrane. Calls were recorded on a Marantz PMD 420 cassette tape recorder, and subsequently analyzed with a Kay DSP Model 8500 Monograph and a Data 6000 wave form analyzer. The microphone and amplifier was built to the specifications of H. C. Bennett-Clark [J. Exp. Biol. 108, 459 (1984)].
9. Caterpillar calls were all of sufficiently low amplitude as to be detectable only by employment of the particle velocity microphone. As suggested by DeVries (4), it is likely that all calls are produced when the shafts of the vibratory papillae drag across the granulations on the head when the caterpillar oscillates its head in and out.
10. Frequencies were measured for 76 individual pulses taken from 20 individual walking caterpillars: 15 fifth instar caterpillars (11 individuals, 4 pulses; 1 individual, 5 pulses; 3 individuals, 2 pulses; and 1 individual, 1 pulse), and five fourth instar caterpillars (4 pulses each).
11. Two-day-old individual caterpillars ranging from third to fifth instar had both vibratory papillae removed with finely pointed forceps. After subsequent testing with the particle velocity microphone, all caterpillars were allowed to molt, rested for sound production, and depending on the instar, had their vibratory papillae removed again. An additional 10 antennal segments in third instar had only a single vibratory papilla removed and were tested for their ability to produce sound.
12. To test if T. ventralis caterpillar calls were attractive to ants, two sets of experiments were performed with field-collected caterpillars that were paired by instar and size before experimentation. One set was performed in an ambient temperature laboratory using captive ant colonies and potted plants (n = 16 pairs), and the other set was performed in the field with naturally occurring plants and ant colonies (n = 35 pairs). In each pair of caterpillars, one individual had the vibratory papillae removed, whereas the other individual retained them. Pairs of caterpillars were placed on individual plants where all caterpillars and ants had been removed immediately before experimentation. The pairs were then censused simultaneously for the number of ants tending each caterpillar at time intervals ranging from 1 to 12 hours, and each pair was left on the plant for 1 to 4 days of censuses. During the study each plant had only the paired caterpillars on it. All experiments used the same species of ant, Ectatomma ruidum (Ponerinae), and all caterpillar pairs were either fourth or fifth instars. The cumulative numbers of ants tending caterpillar pairs were compared by a Wilcoxon signed-pairs test.
13. Quantifying the attenuation of substrate-borne signals is problematic because signal attenuation varies with substrate, the dispersion rate, frequencies, and type of waves produced and the distance from signal [See M. Gogala (20)]. The natural substrate caterpillars and ants live on is a combination of leaves, petioles, stems, bark, and soil—all with varied physical properties. Yet on these types of substrates, insects may receive directional information from vibrational signals with frequencies similar to those found in caterpillar calls (see M. Gogala (20)). Although there is little doubt that natural substrates have different transmission properties than the substrate on which calls were recorded (6), it is likely (but not yet tested) that ants could receive caterpillar calls from distances of 5 cm on a variety of substrates.

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Allometric Engineering: An Experimental Test of the Causes of Interpopulational Differences in Performance

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Hatching lizards (Sceloporus occidentalis) from a southern population are large and have high locomotor performance (speed and stamina) relative to hatchlings from northern populations. In order to determine whether differences in performance are an allometric consequence of interpopulation differences in size, yolk was removed from southern eggs, thereby producing miniaturized hatchlings equivalent in size to northern hatchlings. Miniaturized southern hatchlings no longer had higher speed than northern hatchlings, but maintained higher stamina. Interpopulation differences in speed but not in stamina are thus an allometric consequence of differences in egg size. Size manipulation adds an experimental dimension to allometric analyses.

Ever since Huxley (1) first drew attention to the biological significance of relative size and shape, evolutionary and functional biologists have studied the allometric scaling of diverse morphological, physiological, and ecological traits (2). Allometric equations not only quantify the size dependence of a trait, but can also permit comparisons among individuals, populations, or species (3, 4) that differ in body size. Consequently, allometric analyses are often a key step in tests of hypotheses of trait evolution (2–5). Nevertheless, such analyses involve statistical, not experimental, adjustments of body size (6). Moreover, inferences about the proximate or mechanistic causes of dramatic differences in the intercept and slope of the allometry among taxa are risky, because many factors influence morphological and physiological traits (7).

Here we apply a novel method for experimentally manipulating body size, and we use this method to explore the mechanistic bases for interpopulational differences in the al-
ometry of locomotor performance and morphology of hatching lizards (Sceloporus occidentalis). Compared with hatchlings from northern populations (Oregon and Washington), hatchlings from a southern population (California) are large, have long hind limbs, and have high burst speed and cruising stamina (Figs. 1 and 2). The high locomotor performances of southern hatchlings might be a mechanistic consequence of large body size (Fig. 1), of relatively long limbs (8) (Fig. 2A), or of other physiological or morphological differences. The involvement of these factors can potentially be tested at least three ways. First, the small northern hatchlings could be raced once they had grown to the size of (large) southern hatchlings, but this comparison would confound size and age. Second, analysis of covariance can often be used to determine if differences in a trait persist when body size is adjusted statistically, but such analyses may be misleading because causal factors responsible for trait divergence among populations may be different from the factors determining allometric scaling among individuals within a population. Third, between-popu-

Fig. 1. Frequency distribution for body mass of unmanipulated hatchlings (solid bars, triangle indicates mean size) from Washington (n = 87); Oregon (n = 143); and California (n = 61) and for size-reduced hatchlings (light shading) from California (n = 78); dense shading indicates the size of unmanipulated sibs. Populations are significantly different with respect to unmanipulated hatchlings [ANOVA: F(2,288) = 115.6, P < 0.001]. Whereas the means of unmanipulated Washington and California hatchlings differ by more than three standard deviations, unmanipulated Washington hatchlings and size-reduced California hatchlings overlap broadly in size and the means are nearly identical.

Fig. 2. (A) The allometry between hatching mass (grams) and hindlimb span (millimeters). The population regression lines (solid) and geometric means (squares) are provided for all three populations (Washington (Wa), Oregon (Or), and California (Ca)) (x- and y-axes are logarithmic). The allometric equations relating the scaling between hindlimb span (HLS) and body mass (m) are as follows. Washington: HLS = 42.5m^{0.319} (SE for slope = 0.024, n = 80); Oregon: HLS = 42.1m^{0.362} (SE for slope = 0.019, n = 78); California: HLS = 47.7m^{0.318} (SE for slope = 0.038, n = 25); and experimentally reduced California hatchlings (and control sibs): HLS = 46.3m^{0.271} (SE for slope = 0.025, n = 52, 95% confidence intervals also provided). The allometry between body mass (g) and (B) stamina (minutes) = 4.93m^{0.466} (SE for slope = 0.443, P = 0.06) and (C) burst speed (centimeters per second) = 152m^{0.434} (SE for slope = 0.094, P < 0.01); for miniaturized California hatchlings and their full-sized sibs (regression line with 95% confidence limits for a new mean). Squares represent the geometric (log-transformed) means (with SE) for mass and each performance trait for unmanipulated individuals from Washington (Wa) or Oregon (Or) and hatchlings from California (Ca). Triangles represent the geometric means pooled for various size classes of hatchlings resulting from varying degrees of size manipulation [100% (n = 7, unmanipulated; n = 15, sham-manipulated), 70 to 90% (n = 18), 60 to 70% (n = 12), and 50 to 60% (n = 5) of original egg mass remaining after yolk removal].
turized hatchlings from California still had much higher stanima than did those from Washington but not hatchlings from Oregon (15) (Fig. 2B). Thus, significant inter-population differences in stanima of hatchlings, though in part an allometric consequence of differences in egg and hatching size, are in large part due to other mechanistic causes, presumably those affecting aero-

bic capacity (4, 16).

In contrast, inter-population differences in burst speed disappeared when body size was standardized and thus were causally related to inter-populational differences in egg size and thus hatching size (Fig. 2C). Miniaturized southern hatchlings were no faster than were similarly sized northern hatchlings (17). Moreover, because mini-

turized southern hatchlings from California still had longer legs (18) (Fig. 2A) but not faster speeds (Fig. 2C) relative to northern hatchlings, inter-populational differences in burst speed are unlikely to be purely a mechanistic consequence of differences in relative hindlimb length, despite presumed biomechanical links between these traits (4, 8).

Developmental manipulation of body size (“allometric engineering”) adds to comparative biology a powerful new experimental dimension that can be used with diverse taxa (9, 19). Adult size can also be manipulated by the use of genetic engineering of the hormonal control of growth rate (20). However, this technique can currently be applied in only a few taxa. Size manipulation by either technique may allow comparisons between populations with limited overlap in body size (21), thereby permitting inferences on the proximate causes of trait evolution. Moreover, both techniques provide a direct experimental, not merely statistical, evaluation of the proximate influence of body size. For example, manipulation of hatching size shows that inter-populational differences in sprint speed are probably an allometric consequence of inter-populational differences in egg size, but that inter-populational differences in stanima and morphology, though in part due to size, necessarily involve additional evolved factors (4, 16, 22). A comparison of experimental with traditional analysis of covariance (ANCOVA) analyses (15, 17, 18) demonstrates that purely statistical analyses of patterns can sometimes present a misleading portrait of the role of body size in populational differ-

entiation in locomotor performance and morphology. Of course, size manipulation (9, 19, 20) provides insights only into proximate—not ultimate—causes of inter-populational varia-

tion in traits. For example, our results do not suggest whether contemporary inter-

populational patterns reflect natural selec-

tion in southern populations for large size or fast speed or both. Nevertheless, size ma-

nipulation does show that selection on size alone is unlikely to account for all the major inter-populational differences in locomotor performance (or the converse). Moreover, if the relative fitness of size-manipulated animals is measured in natural populations, some in-

sights into the ultimate causes of inter-populational variation can be gained (9, 23).

REFERENCES AND NOTES

2. Allometric equations are power functions of the form y = ax^n, where n is usually body size (mass). S. J. Gould, Biol. Rev. 41, 587 (1966); W. A. Calder, Size, Function and Life History (Harvard Univ. Press, Cambridge, MA, 1984); R. H. Peters, The Ecological Implications of Body Size (Cambridge Univ. Press, Cambridge, 1983); R. Schmidt-Nielsen, Scaling: Why Is Animal Size So Important (Cam-

6. Because different curve-fitting models often yield different results, any conclusions may be model dependent (M. D. Pagel and P. H. Harvey, Science 244, 1589 (1989)).
8. In general, speed and stanima are typically correlated with body size within populations. Moreover, long hindlimbs are thought to enhance speed by increasing stride length [V. B. Sukhanov, General System of Symmetrical Lossassm of Terrestrial Vertebates and Some Features of Movement of Lower Tetrapods (Nal’sk, Leningrad, translation into English by Am-

10. Near-term, gravid females were collected near Wrightwood, CA, on the east side of Table Moun-

tain (altitude, 2230 m), near Terrebonne, OR (750 m), and near Lyle, WA (200 m).

11. Ten to 50% of total egg mass was removed with a 26” sterile syringe (n = 13 clutches). Incubation success of sham-manipulated controls and size-re-

duced eggs is similar, ~70%, as is post-hatching survival in the laboratory (9). Size reduction does not artifically influence growth rate (9). More-

over, because the size-reduced lizards from Califor-

nia still pass the gross morphological test of physiologic capacity, size-reduction does not ap-

pear to hamper performance artificially.

12. Washington (n = 7 clutches), Oregon (n = 16 clutches) and Idaho (n = 14 clutches). The offspring from unmanipulated clutches obtained from California females were comparable to the sham-

manipulated offspring from the unmanipulated controls obtained from experimentally manipulated clutches (11) with regard to hatching size (Fig. 1), speed, and stanima of Fig. 2 and B and C.

13. Hindlimb span (millimeters measured between the fourth toe on each hind leg with hind legs stretched out laterally to either side).

14. To determine “crushing stamina” we placed hatchlings on a rubberized belt of a treadmill moving at 0.25 km/hour. When necessary to keep them run-

ning smoothly, we tapped them lightly on the tail and hindlimbs. Stamina was measured as the elapsed time (minutes) until a hatchling was exhausted, as verified by the loss of the righting response [F. H. van Berkum, R. B. Huey, J. S. Tsuij, T. Garland, Jr., Funct. Ecol. 3, 97 (1989)].

15. Because the size of Oregon hatchlings and miniatur-

ized hatchlings from California was similar, these populations could be compared without the con-

ounding effects of size. This ANCOVA (log-transformed variables) indicated that the difference in stanima between California and Oregon hatchlings [0.25 log (min)] was not significant [F(1,178) = 2.92, P = 0.12; covariate for size (ns), F = 0.16; covariate for stanima (ns), F = 0.52; covariate for size and stanima (ns), F = 0.16]. ANCOVA comparing Washington hatchlings and experimentally miniaturized hatch-

lings from California indicated that the difference in stanima and population size was not significant [F(1,86) = 20.98, P < 0.0001; covariate for size, ns, F = 0.81]. It is illuminating to compare the results obtained from this experimental analysis with a purely statistical analysis in which traditional AN-

COVA of the data from the unmanipulated popula-

tions samples was used. The traditional ANCOVA indicated that the difference in stanima between Oregon and California populations (0.41) was sig-

nificant [F(1,82) = 7.77, P < 0.007; covariate for size, ns, F = 0.68], as was the difference between Washington hatchlings and unmanipulated hatch-

lings from California [difference, (0.80); F(1,90) = 48.82, P < 0.0001; covariate for size, ns, F = 0.08]. However, the population compari-

sons with traditional ANCOVA overestimated the level of population differentiation, because a signifi-

cant allometric effect of size on stanima was not detected in these analyses in contrast to analyses using the full range of size-manipulated hatchlings [F(1,65) = 3.82, P = 0.06, n = 47 (Fig. 2B)]. Meanwhile, the analysis demonstrates that mini-

turized hatchlings is not sensitive to problems aris-

ing from ANCOVA estimates of the allometric slope (6), because the differentiation in stanima is closely matched in contrast to traditional ANCOVA population comparison.


17. A comparison (ANCOVA of log-transformed data) of the burst speed of size-matched hatchlings from California with hatchlings from other northern populations indicated that differences in each popu-

lation were not significant [difference between Califor-

nia and Oregon, F(1,144) = 0.66, P = 0.50; covariate body mass, ns, F = 0.90; difference between California and Washington, ~0.006 log (ms). F(1,151) = 0.33, P = 0.58; covariate body mass, ns, F = 0.96; covariate for size, F(1,151) = 0.03. In contrast, traditional ANCOVA using data from the unmanipulated popula-

tion samples indicates that southern and northern hatchlings are significantly different [difference between California and Oregon, 0.077; F(1,134) = 4.663, P = 0.03; covariate body mass, ns, F = 0.95; difference between California and Washington, 0.066; F(1,134) = 3.178, P = 0.07; covariate for body mass significant, P = 0.03]. However, the population comparisons using tradi-

tion
Induction of AIDS in Rhesus Monkeys by Molecularly Cloned Simian Immunodeficiency Virus

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Better understanding of the pathogenesis of acquired immunodeficiency syndrome (AIDS) would be greatly facilitated by a relevant animal model that uses molecularly cloned virus of defined sequence to induce the disease. Such a system would also be of great value for AIDS vaccine research. An infectious molecular clone of simian immunodeficiency virus (SIV) was identified that induces AIDS in common rhesus monkeys in a time frame suitable for laboratory investigation. These results provide another strong link in the chain of evidence for the viral etiology of AIDS. More importantly, they define a system for molecular dissection of the determinants of AIDS pathogenesis.

Identification of the genetic determinants of oncogenesis and tissue specificity of type C retroviruses has been achieved largely through the use of cloned DNA capable of yielding pathogenic virus (1). Human immunodeficiency virus (HIV), the causative agent of AIDS, is a member of the lentivirus subfamily of retroviruses. Although much has been learned about the molecular biology of HIV, systems for study of disease induction by molecularly cloned HIV have not been developed. In fact, there have been no previous reports of disease induction by a molecularly cloned lentivirus from any species.

The simian immunodeficiency viruses (SIVs) are nonhuman primate lentiviruses that are the closest known relatives of HIV-1 and HIV-2. They closely parallel their human counterparts in genetic organization and biological properties (2). Similarities between HIV and SIV include lentiviral morphology, tropism for CD4 lymphocytes and macrophages; extra genes called tat, rev, vpx, vpr, and nef; other retroviruses do not have; use of the CD4 molecule for receptor; cytopathicity; and the ability to cause chronic disease after long-term persistent infection. Infection of common rhesus monkeys (Macaca mulatta) with some isolates of SIV results in AIDS and death in a time frame suitable for laboratory investigation (3). Features of the AIDS-like disease induced by SIV include CD4 lymphocyte depletion, opportunistic infections, severe weight loss, opportunistic neoplasms, and a multifocal granulomatous encephalitis. These are also features characteristic of HIV-induced disease in humans. The similarity in genomic organization, the extensive sequence homology, and the similarity in

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Fig. 1. Antibody responses in rhesus monkeys inoculated with SIVmac239 cloned virus. Portions of plasma from blood samples were frozen at −70°C on the weeks after inoculation and analyzed at a 1:20 dilution for antibodies to SIV by enzyme-linked immunosorbent assay (ELISA) as previously described (6, 9, 19). The five animals shown were inoculated with virus produced in macaque PBLs (8). The symbols used to identify the rhesus monkeys are ○, 316-85; ●, 452-87; □, 54-83; ▲, 326-87; and △, 124-79.