

A. PROJECT SUMMARY

Evolutionary adaptation at the phenotypic level is a complex process that involves changes, at multiple levels of biological organization, in response to manifold selective factors. Although scientific studies typically examine only a limited set of phenotypic attributes, organisms nevertheless evolve as integrated wholes, not just one piece at a time. Hence, during phenotypic evolution, complex sets of allied traits ("adaptive suites") can emerge. As well, morphological and physiological mechanisms can cause functional trade-offs among higher-level traits. For example, several authors have suggested that (1) a wide range of morphological, physiological (including locomotor), and ecological traits are consistently associated with foraging mode, and that (2) variation in muscle fiber-type composition or limb morphology should cause a trade-off between locomotor speed and stamina. Because of such complexities, elucidation of adaptation requires information from a wide range of methodological approaches aimed at multiple levels of biological organization. Of the many approaches to studying adaptation, interspecific comparisons, conducted within a phylogenetic framework, are the only way to test hypotheses about long-term evolution of traits that do not fossilize. Measurement of whole-organism performance abilities (e.g., maximal sprint running speed, endurance) is especially important for studying adaptation, because performance transduces the effects of lower-level traits (e.g., muscle physiology) to higher levels (e.g., behavior) upon which selection acts most directly.

This renewal proposal aims to use lizard locomotion, studied in a phylogenetic context, to address two main issues. First, it will build on the previous NSF grant to expand understanding of how organismal performance, measured in the laboratory, is affected by lower-level morphological and physiological traits. Second, it will broaden the scope of investigation by examining relationships between locomotor performance in the lab and locomotor behavior quantified in the field. Two general hypotheses will be tested: (1) subordinate traits, such as muscle contractile properties, affect locomotor performance measured in the laboratory under controlled conditions; (2) performance abilities can predict among-species variation in the actual locomotor behavior of animals in the field. The study will concentrate on 12 species within the family Phrynosomatidae, for which extensive locomotor and physiological data already exist. This well-studied clade contains three subclades, which differ substantially in physiology, morphology, laboratory locomotor performance, and field locomotor behaviors. Five additional species will be used as outgroups.

Existing and new data will span the range from biochemistry (e.g., muscle enzyme activities), through whole-organism performance in the laboratory (e.g., maximum sprint speed), to locomotor behavior in the wild (e.g., speed while foraging). In addition, data available in the literature will be used to examine the same range of traits in a wider range of species, although with some loss of precision. Preliminary results, mostly based on data gathered under the previous grant, are very promising. Regarding the first hypothesis, they indicate that some lower-level traits (e.g., muscle fiber-type composition, relative hindlimb length) strongly affect certain aspects of locomotor performance (in this case, sprint speed) but not others (in this case, endurance). Regarding the second hypothesis, they suggest that lizards which move infrequently in the field may also have relatively low endurance as measured in the laboratory.

This integrative, multilevel research will take advantage of unique expertise offered by collaboration of the principal investigator, Theodore Garland, Jr., the postdoctoral research associate, Gad Perry, Todd T. Gleeson (University of Colorado), and Robert K. Josephson and Albert F. Bennett (University of California-Irvine). Garland has expertise in measurement of lizard locomotor performance and in phylogenetically based statistical methods. Perry has expertise in measurement of field locomotor behaviors. Gleeson will perform muscle enzyme assays on the previously gathered tissues, at minimal cost to this proposal. Josephson and Bennett will host the muscle contractile work. The research will also provide broad-based training opportunities for two graduate students (one is currently supported by an NSF Graduate Research Fellowship to conduct comparative analyses of variation in lizard blood oxygen carrying capacity; a second [to be named] will conduct the muscle contractile work at Irvine). Overall, this study will improve understanding of the coadaptation and complex interactions of morphological, physiological, and behavioral traits related to locomotion, while also setting the stage for exciting future research.

C. 1. RESULTS FROM PRIOR NSF SUPPORT (IBN-9723758) - Theodore Garland, Jr. - P.I.

This is a renewal for IBN-9723758, "Morphological and Physiological Correlates of Locomotor Performance in Phrynosomatid Lizards," which was submitted 10 Jan. 1997. That proposal requested \$84,224 over a period of 36 months, but was funded at \$40,000 total costs. With the budget reduction, the sub-award to the co-PI Todd T. Gleeson (Univ. of Colorado) was eliminated, and he participated in the research at minimal cost to the grant (supplies only). Including a 1-year no-cost extension, research has been conducted 15 Aug. 1997 - 31 July 2000. Specific Aims were broadly similar to those of this renewal, but did not include measurement or field behaviors nor muscle contractile properties. In accordance with the budget reduction, we reduced the goals. We concentrated on measuring locomotor performance and on sectioning and staining thigh muscles for analysis of fiber-type composition. We obtained data for 29 species from 7 families (sensu Frost and Etheridge [1989]) This includes 291 individuals for performance, 228 for organ masses and hematocrit, and 189 whose thigh muscles were prepared as microscope slides for histochemical analysis of muscle fiber-type composition. Analysis of these slides is ongoing.

Major results to date are: (1) Maximal sprint speed on a high-speed treadmill (a new technique), is highly repeatable and positively correlated with relative hindlimb length (Bonine and Garland, 1999). (2) Photocell-timed racetracks, the traditional way of measuring sprint speeds, may underestimate maximal speeds of fast species (Bonine and Garland, in prep.). (3) Treadmill endurance, measured at 1.0 km/h, predicts some field behaviors (Garland, 1999). This important result validates the "ecological relevance" of one of our main measures of performance. In a related study completed under this grant (Clobert et al., 2000), we found that individual variation in treadmill endurance predicts parasitism and activity rate, but not survivorship, in a population of lacertid lizards; hence, individuals with low endurance seem to be able to "compensate" behaviorally for their lower performance abilities. Together, these results motivate our proposed expansion of scope, to also examine the field-behavioral correlates of speed and endurance.

(4) We discovered that phrynosomatid lizards show an amazing range of variation in muscle fiber-type composition (Bonine et al., 1997, 2000, in review). Based on the 11 species analyzed to date (Fig. 6), *Sceloporus*, which are "typical" lizards in many ways, also show "typical" muscle composition, e.g., the iliofibularis (IF) contains on average about 45% fast-twitch glycolytic (FG) fibers. In striking contrast, sand lizards, which are fast sprinters (Fig. 2) with long legs (Fig. 4), have more than 65% FG fibers. This makes them the saurian equivalent of the cheetah, which also has a high percentage of FG fibers (Williams et al., 1997). The sister group of the sand lizards, the horned lizards (genus *Phrynosoma*; see Fig. 1) have only 25-30% FG fibers, short legs, and are slow sprinters. The interspecific differences in % FG fibers are strongly inversely related ($r = -0.951$) to % fast-twitch oxidative glycolytic (FOG) fibers (range = 25-66%), with the percentage of slow-twitch oxidative (SO) fibers ranging from < 1% in *Callisaurus draconoides* up to 17% in *Sceloporus magister*. The vast difference in IF fiber-type composition among members of the Phrynosomatidae motivates our current proposal to examine contractile properties of the same muscle.

(5) A conventional multiple regression analysis of the data shown in Figs. 2, 4, 5, 6 (11 species) indicates that **both %FG fibers ($P = 0.0015$, $\text{partial } r^2 = 44\%$) and relative hindlimb length ($P = 0.0131$, $\text{partial } r^2 = 20\%$) are significant predictors of sprint speed.** (6) Treadmill endurance is significantly positively associated with body mass and marginally with % SO fibers ($r = 0.543$, 2-tailed $P = 0.084$), but not with hindlimb span, hematocrit, heart mass or liver mass. Neither total thigh nor iliofibularis muscle cross-section is a predictor of either speed or endurance. (7) Contrary to predictions, speed and endurance are not negatively related (appear to trade-off) for the preliminary set of 11 phrynosomatid species.

(8) We have documented other aspects of physiological and morphometric variation in phrynosomatids. The three phrynosomatid subclades do not show a clear separation in endurance running capacity, although endurance is positively related to body size (Fig. 3). Horned lizards show relatively small thigh muscles (Fig. 5) and low hematocrit (Fig. 7). Sand lizards, on the other hand, have relatively small hearts (Fig. 8). Horned lizards tend to have large livers (Fig. 9), which may reflect their dietary specialization on ants or possibly storage of glycogen or lipids (discussion in Garland, 1993); in any case, liver mass or enzyme activity may be related to endurance (Garland, 1984; Garland and Else 1987).

Here, we propose to complete work begun under the previous award while gathering new data on field locomotor behavior, as well as enzymatic activities and both isometric and isotonic contractile properties of the iliofibularis muscle. We will eliminate some outgroups and concentrate on species within Phrynosomatidae (see **Fig. 1**), as was strongly recommended by reviewers of the previous proposal. We will study the same populations as before (see Garland and Adolph, 1991). Together with the existing data, this will allow a reasonably comprehensive analysis of the correlated evolution of locomotor behavior, performance, and underlying morphological and physiological traits that determine locomotor abilities.

Development of Human Resources:

Kevin E. Bonine used Bonine and Garland (1999) for his M.S. in Zoology; the rest of the work under the previous award forms the basis for his Ph.D. dissertation, to be completed during summer 2001. He completed sample collection during the summer of 1999, finished slicing and staining all muscles (with T. T. Gleeson) in June of 2000, and is now analyzing the fiber-type slides. Dr. Gad Perry was hired as a postdoc for four months, during which he collected animals for us in Texas and Israel, obtained preliminary data on field behaviors, compiled the data on home ranges for Perry et al. (in preparation), and completed a study of the allometry of sexually dimorphic traits in *Anolis cristatellus* (Perry and LeVering, in review). Three undergraduates participated in the research. Emily J. Baker assisted in Boulder during the summer of 1997, subsequently completed a Master's in T. T. Gleeson's lab, and is now a research assistant in another lab in Boulder. Geoff R. Hosack assisted in Madison during the summer of 1999 and is now in graduate school at the University of Washington. Anna M. Hansen assisted in Boulder during summer 2000, and is now developing an honor's thesis project in T. T. Gleeson's lab; most likely, she will focus on the proposed enzyme assays, as described below and in T. T. Gleeson's letter of collaboration (attached).

The PI uses examples from this research in both courses that he teaches, "Evolutionary Biology" (Zoology/Botany/Anthropology 410) and "Evolutionary Physiology" (Zool. 545). Many of the hypotheses and results are fairly easy for undergraduates to grasp (e.g., fast sprinters should have long legs and many fast-twitch muscle fibers). Photos of such strange animals as horned lizards and their desert habitat, along with descriptions of their unusual biology, are a big hit in class and truly seem to facilitate learning.

Publications Acknowledging Support from IBN-9723758:

- Bonine, K. E., and T. Garland, Jr. 1999. Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. *Journal of Zoology, London* 248:255-265.
- Bonine, K. E., and T. Garland, Jr. In preparation. A comparison of maximal sprint running speeds of lizards as measured on a racetrack and a high-speed treadmill.
- Bonine, K. E., T. Garland, Jr., and T. T. Gleeson. 1997. Muscle fiber-type variation and locomotion in phrynosomatid lizards. *American Zoologist* 37(5):104A. [presented at Jan. 1998 S.I.C.B. meeting]
- Bonine, K. E., T. T. Gleeson, and T. Garland, Jr. 2000. Fiber-type variation in the iliofibularis muscle of phrynosomatid lizards. *The Physiologist*. In press. [poster for Sept. 2000 A.P.S. Conference]
- Bonine, K. E., T. T. Gleeson, and T. Garland, Jr. In review. Fiber-type variation in the iliofibularis muscle of phrynosomatid lizards. *Journal of Morphology*.
- Clobert, J., A. Oppliger, G. Sorci, B. Ernande, J. G. Swallow, and T. Garland, Jr. 2000. Endurance at birth predicts parasitism level and activity rate later in life in the common lizard. *Funct. Ecol.* In press.
- Garland, T., Jr. 1999. Laboratory endurance capacity predicts variation in field locomotor behaviour among lizard species. *Animal Behaviour* 58:77-83.
- Kohlsdorf, T., C. A. Navas, and T. Garland, Jr. In revision. Limb and tail lengths in relation to substrate usage in *Tropidurus* lizards. *Journal of Morphology*.
- Perry, G., and K. R. Levering. In review. Identifying sexually selected traits from allometry in the lizard *Anolis cristatellus* Dumeril and Bibron (Iguania). *Biological Journal of the Linnean Society*.
- Perry, G., T. Garland, Jr., and J. G. Swallow. In preparation. Factors affecting home-range size in lizards: body size, habitat type, diet, and phylogeny. Intended for *Ecology*.

C. 2. SPECIFIC AIMS

Elucidation of evolutionary adaptation typically requires information from multiple levels of biological organization (Rose and Lauder, 1996; Schmitt, 1999), yet a lack of comprehensive data inhibits such synthetic analyses for most organisms. We propose to take advantage of the unusual concentration of information on lizard locomotor biology to conduct a hypothesis-driven, multidisciplinary study of the correlated evolution of locomotor traits, framed in a phylogenetic context.

Both theory (e.g., Huey and Pianka, 1981; Vitt and Price, 1982; Autumn et al., 1999) and a relatively large body of empirical knowledge exist concerning lizard locomotor biology. Data are available on whole-animal performance, underlying morphological traits and physiological processes, and possibly correlated field behaviors and ecological factors. Despite this, many existing predictions regarding coadaptation of lizard locomotion remain untested or only weakly supported (Losos and Sinervo, 1989; Perry and Pianka, 1997; Garland, 1999; Irschick and Losos, 1999). This renewal proposal will seek to elucidate interrelated sets of traits (possible "adaptive suites"), ranging from the level of biochemistry (enzymatic activities in muscles) to ecology (home range size). It will encompass both links in the Morphology → Performance → Behavior paradigm (see Section 1 of Background). Based on current information, we can make a series of specific predictions. For example, regarding Morphology → Performance relationships (the focus of the previous grant), we predict that muscle contractile properties will be predictive of maximal sprint running speed; regarding Performance → Behavior relationships (a major expansion of the current proposal), we predict that species with high endurance should also have large home range sizes. We will compare lizard species to achieve the following specific goals:

1. Test the hypothesis that limb and tail proportions and/or muscle properties (fiber-type composition, enzyme activities, *in vitro* contractile properties) predict variation in maximal sprint running speed.
2. Test the hypothesis that the same lower-level traits, plus indices of cardiovascular function (heart mass, hematocrit), predict interspecific variation in running endurance capacity (stamina).
3. Determine the relationship between locomotor speed and endurance, and how it is mediated by subordinate morphological and physiological traits.
4. Test the hypothesis that locomotor performance predicts variation in field locomotor behavior.

Some of the necessary data already exist (e.g., limb and tail morphometrics, speed and endurance) or will soon be available (e.g., muscle fiber-type composition). We will collect new data on both lower-level (muscle enzyme activities and contractile properties) and higher-level (field locomotor behavior) traits. 17 species are chosen for intensive study (see **Fig. 1**), including five outgroups and 12 in the phenotypically diverse (**Figs. 2-11**) but closely related Phrynosomatidae. All 17 are easily accessible, and their phylogeny is well understood. Strong inference will result from phylogenetically based statistical analyses of the multi-level phenotypic data, thus allowing identification of suites of coadapted traits. Our preliminary data show that the three phrynosomatid subclades differ greatly in many of the attributes slated for study (**Figs. 2-11**), and that some of these features indeed appear to form integrated suites (**Fig. 1**). They also indicate that sprint speed can be accurately predicted from relative hindleg length and muscle fiber-type composition. A larger dataset, drawn primarily from published studies, will be used to address these issues with greater breadth but, because the sources of information are heterogeneous, less precision. This will allow expansion of the phylogenetic range of coverage and inclusion of traits, such as home range size, that would not be feasible to measure within the context of the current proposal.

The proposed work will take advantage of unique and complementary expertise offered by the collaboration of five senior personnel (Theodore Garland, Jr. [PI], Gad Perry [Postdoc], Todd T. Gleeson, Robert K. Josephson, and Albert F. Bennett) to conduct an integrative, multilevel research program. It will also provide broad-based training opportunities for two graduate students (one already supported by an NSF Graduate Research Fellowship). Thus, our study will deepen understanding of the impact of subordinate morphological and physiological traits on locomotor performance, and broaden the scope of the previous grant by examining the relationship of performance abilities to behavior quantified in the field.

C. 3. BACKGROUND

1. Morphology → Performance → Behavior → Fitness. The Morphology → Performance → Fitness paradigm was proposed by Arnold (1983) as a conceptual and analytical framework for the study of adaptation. He argued that one important way to study adaptation was to measure ongoing selection in natural populations. This could be done by determining whether individual variation in phenotypic traits correlated with variation in Darwinian **Fitness** (unfortunately quite complicated to measure; e.g., McGraw and Caswell, 1996) or major components thereof (e.g., survivorship, fecundity). "**Morphology**" was used as a shorthand for various sub-organismal traits, including body proportions, physiology, and biochemical characters. Such lower-level traits determine whole-animal **Performance** abilities (e.g., locomotor speed or stamina), which are seen as being closer to the direct effects of natural or sexual selection.

Arnold (1983) did not specifically address the place of behavior, except to consider it as another possible factor that could affect performance. This role is taken away if performance is measured under conditions of maximal motivation, as has been presumed by many subsequent workers. This also allows us to elevate the status of **Behavior**. Hence, the $M \rightarrow P \rightarrow F$ paradigm has been expanded to explicitly reflect the crucial "filtering" role of behavior, i.e., $M \rightarrow P \rightarrow B \rightarrow F$ (Garland et al., 1990; Garland, 1994b; Garland and Carter, 1994; Garland and Losos, 1994). For example, an animal faced with a predator may freeze, stand and fight, run away at top speed, or slink away at a lower rate. Most likely, which behavior is employed depends on both the abilities of the individual and the specific circumstances. Behavior can thus play a crucial role in mediating between maximum achievable performance, typically measured in the laboratory (see Garland, 1994a; Garland and Losos, 1994), and what selection "sees" under field conditions. Although many variants of the general paradigm are possible, all of them serve as powerful heuristics in modern integrative organismal biology (e.g., Feder and Watt, 1992; Wainwright, 1994).

The Morphology → Performance → Behavior → Fitness paradigm can also be extended to among-population or among-species variation (Emerson and Arnold, 1989; Schluter, 1989; Garland and Losos, 1994). Phenotypic differences among species can result from several processes, but only natural selection is likely to produce a correlation between phenotype and environment. Hence, such correlations are taken as evidence that past selection has played a role in shaping the current differences among species (Brooks and McLennan, 1991; Harvey and Pagel, 1991; Eggleton and Vane-Wright, 1994; Garland and Adolph, 1994; Losos and Miles, 1994; Martins, 1996c; Rose and Lauder, 1996; but see Leroi et al., 1994, and responses by Doughty, 1996; Larson and Losos, 1996:210-217). We propose to gather and to integrate both physiological and ecological data, thus examining both the Morphology → Performance (focus of the previous grant) and the Performance → Behavior links, in comparative studies of different lizard species.

A general tenet of both physiology and evolutionary biology is that complex interactions among traits that form a functional complex can strongly affect future responses to selection (e.g., see Price and Langen, 1992). As a result, member traits may have a limited number of possible states (for examples, see e.g., Brown and Lasiewski, 1972; Pianka, 2000, pp. 100-103; Wagner and Schwenk, 2000). Because such sets of traits can have a high level of interdependency, complex organisms may take longer to adapt than ones in which complexity is low and fewer traits need simultaneously be accommodated (Orr, 2000). Related to the idea of functional complexes, many biological examples demonstrate that different "solutions" may exist to common environmental challenges (= selective regimes). Accordingly, evolution may have produced lizard species with different suites of correlated locomotor and behavioral traits. Our emphasis on the ingroup of phrynosomatid lizards while also considering some key, and very different, outgroup taxa (see Fig. 1), should allow us, if they exist, to uncover "multiple solutions" by which adaptive evolution has attained functional equivalence (Bock, 1977; Emerson, 1984; Bartholomew, 1987; Emerson and Koehl, 1990; Alexander, 1991; Sinervo et al., 1992; Wistow, 1993; Arnold, 1994, 1995).

2. Lizard Locomotion as a Model System. Lizards have often served as model organisms (Milstead, 1967; Huey and Pianka, 1981; Huey et al., 1983; Moermond, 1986; Vitt and Pianka, 1994). Extant lizards are relatively speciose (over 3,300 species [excluding snakes]; Pough et al., 1999) and are locally abundant in many ecosystems (e.g., Pianka, 1986). Depending on the species, lizard locomotion encompasses not

only quadrupedal gaits but also bipedality, gliding, limblessness, specialized toe pads, toe fringes, and the ability to run across water (Zug, 1993). As in other lineages (e.g., birds), locomotor modes and abilities may represent key innovations related to species and/or phenotypic diversity. For example, Warheit et al. (1999) compared the morphometric disparity of *Anolis* and *Sceloporus* (one of our ingroups) and suggested that the morphological innovation of toe pads (which affects climbing and clinging ability) allowed anoles to invade environments not available to other lizards, which in turn facilitated their great diversification.

Many species of lizards are cooperative subjects in the laboratory, which facilitates measurement of locomotor performance. Morphological and physiological mechanisms underlying locomotor diversity of lizards are themselves varied (Garland and Losos, 1994; Miles, 1994a; Gans et al., 1997; Bonine and Garland, 1999; Irschick and Jayne, 1999; Bonine et al., in review). Lizard field behaviors related to locomotion are also diverse (Stamps, 1977; Christian and Waldschmidt, 1984; Hertz et al., 1988; Garland, 1993, 1999; Cooper, 1995; Irschick and Losos, 1998; Perry, 1999). This variation suggests that locomotion plays an important role in lizard biology, and that locomotor abilities may be causally related to success in many activities that affect Darwinian fitness. At the level of individual variation, for example, Jayne and Bennett (1990) found that survivorship in a natural population of garter snakes was positively related to locomotor speed and distance crawling capacity (see also Brodie, 1992). In laboratory trials involving male *Sceloporus occidentalis* (one of our target species), Garland et al. (1990) found that social dominance was positively related to sprint speed but not to endurance, a result confirmed for *Urosaurus ornatus* by Robson and Miles (2000). Among species, recent work documents morpho-physiological traits that are predictive of locomotor performance (Garland and Losos, 1994; Miles, 1994a; Bonine and Garland, 1999; Irschick and Jayne, 1999), and that field-observed locomotor behaviors are correlated with laboratory performance (Garland, 1999; Irschick and Losos, 1998). We expect that whereas a single set of "solutions" may exist within Phrynosomatidae, other alternatives may appear among outgroup taxa (see Fig. 1). For example, a significant negative relationship exists between sprint speed and treadmill endurance among 12 species of lacertids (Vanhooydonck et al., ms), but not for the phrynosomatids we have studied (see page C-1).

3. Morphology → Performance. Inspired, in part, by Arnold's (1983) $M \rightarrow P \rightarrow F$ paradigm, many ecological and evolutionary physiologists have examined the causes and consequences of variation in locomotor abilities of lizards (reviews in Bennett, 1990, 1991, 1994; Bennett and Huey, 1990; Garland, 1993, 1994; Garland and Losos, 1994; Miles, 1994a,b). Various measures of locomotor performance are possible, including acceleration, speed, distance running capacity, energetic costs, jumping abilities, and stamina. Most typically, measures of speed and endurance are used in an attempt to bracket the range of possible behaviors, from those that rely primarily on anaerobic glycolytic (short, intense bursts of activity) to aerobic (oxidative) metabolism (sustained walking) (see Bennett, 1989; Pough, 1989; Gleeson, 1991). This strategy was followed in our original proposal, and we continue it here.

We will address the relationship between organ-level morpho-physiological traits and whole-animal locomotor abilities of lizards as measured in the laboratory. Our starting point is, therefore, measurement of morphology, physiology, and locomotor performance in multiple species of lizards. We are especially interested in the potential for **trade-offs and constraints** in locomotor biology. Both concepts have played an important role in evolutionary theory (Gould, 1980; Loeschke, 1987; Maynard Smith and Vida, 1990; Antonovics and van Tienderen, 1991; Arnold, 1992). To quote Roff (1992:9): "no creature can do all things: it is bounded by constraints of its genetic architecture, its history, biophysical and biomechanical factors, and its lifestyle." The actual importance of constraints in ecological and evolutionary physiology or behavioral ecology is controversial (e.g., cf. Moermond, 1979a,b; Townsend and Calow, 1981; Calow, 1987; Garland and Huey, 1987; Halliday, 1987; Werdelin, 1987; Wainwright, 1988; Carrier, 1991; Sinervo and Licht, 1991; Losos and Miles, 1994; Fry, 1996; Garland, 1998; Weibel et al., 1988). Furthermore, as noted by Sinervo (1994:1245), "**tests of physiological mechanisms underlying trade-offs are nearly lacking in the empirical literature**" (see also Garland and Carter, 1994; Sinervo and Svensson, 1998).

Many of the factors underlying locomotor abilities are functionally interrelated (see also Emerson, 1985; Emerson and Koehl, 1990). Constraints may, therefore, affect the joint evolution of speed and

stamina. This trade-off prediction arises from biomechanical and physiological principles (e.g., Alexander, 1968; Bennett, 1978; Rome and Lindstedt, 1997; Lindstedt et al., 1998), but many discussions focus on differences among muscle fiber types (see Garland, 1988; Sorci et al., 1995; Dohm et al., 1996; refs. therein). In brief, for a given amount of muscle, variation in the % of fast twitch-glycolytic fibers (better for speed) will relate negatively to the percentage of slow twitch-oxidative fibers (better for stamina). The expectation of a speed-stamina trade-off is bolstered by the observation that Olympic sprinters and distance runners are physically very different (although decathletes are rather good at both: see Garland, 1994:268-270). Several studies have shown trade-offs in lizard locomotor abilities (Huey et al., 1984; Losos and Sinervo, 1989; Sinervo and Losos, 1991; Losos et al., 1993). Most recently, Vanhooydonck et al. (ms.) found a significant negative relationship between sprint speed and treadmill endurance among 12 species of lacertid lizards, using both conventional statistics and phylogenetically independent contrasts. However, analysis of our preliminary data shown in **Fig. 2** and **3** does *not* reveal a similar trade-off in phrynosomatids (see Results from Prior NSF Support). Similarly, sprint and maximal aerobic speeds are uncorrelated among 18 species of mammals (Garland et al., 1988). Our integrative studies of multiple lower-level traits should allow elucidation of how phrynosomatids have broken what simple theory would have predicted should be a "constraint" on the joint evolution of speed and stamina. For example, perhaps variation in the amount of fast twitch-oxidative glycolytic fibers affects both speed and stamina in parallel ways.

Several studies have been successful at demonstrating morphological, physiological or biochemical correlates of *individual variation* in speed or stamina of lizards (e.g., Garland, 1984; John-Alder, 1984; Garland and Else, 1987; Gleeson and Harrison, 1988; Snell et al., 1988; Tsuji et al., 1989; Miles et al., 1995; John-Alder et al., 1996; Macrini and Irschick, 1998). Surprisingly, studies of the correlates of *interspecific variation* in lizard speed or stamina have been largely limited to limb (or tail) proportions (Losos, 1990a,b; Miles, 1994a; Bauwens et al., 1995; Bonine and Garland, 1999; Vanhooydonck et al., manuscript), although Zani (1996) found tail length and caudifemoralis longus muscle length both to be positively related to sprint speed. (Clinging performance has also been examined in some detail [Irschick et al., 1996; Losos, 1990a; Zani, 2000].) Multi-species studies of contractile properties are particularly uncommon (Putnam and Bennett, 1982; see also McLister et al., 1995). Other than Bennett et al.'s (1984) 2-species comparison, no study of lizards has attempted quantitative, multi-species, phylogenetically based tests of the relationships between speed or stamina and most of the traits that we will measure, including muscle contractile properties, fiber-type composition, muscle enzyme activities (see attached letter from T. T. Gleeson), heart mass, and hematocrit (a simple index of blood oxygen carrying capacity).

4. Performance → Behavior. A key characteristic of this proposal is our integrative and multi-level approach. In particular, we propose to expand the scope of previous work to address the largely unexplored question of whether field locomotor behaviors are in fact related to laboratory locomotor performance. This expansion is crucial because the "ecological relevance" of performance measures greatly impinges on their utility for illuminating relationships between morphology/physiology and ecology (Wainwright, 1994; Autumn et al., 1999). Several pathways, including predator avoidance and seeking food or mates, could cause a correlation between locomotor ability and Darwinian fitness. For example, locomotion is crucial for escaping from predators (e.g., for garter snakes in the wild, Jayne and Bennett, 1990; Brodie, 1992; for tadpoles in the lab, Watkins, 1996). However, predation attempts are relatively rare, and gathering data on them is extremely time consuming. Therefore, we shall concentrate on more common locomotor behaviors.

Obtaining food is a major task for most animals (e.g., Stephens and Krebs, 1986; Bell, 1991), and lizards can invest considerable energy in moving about when seeking nourishment (Christian et al., 1997). Of the three papers that began the explicit study of foraging behaviors, two (Emlen, 1966; MacArthur and Pianka, 1966) were primarily theoretical and one (Pianka, 1966) concentrated on lizards. Lizards have been one of the model systems ever since (Perry and Pianka, 1997). Initially, workers divided species into two categories, sit-and-wait and widely foraging (e.g., Huey and Pianka, 1981; McLaughlin, 1989). This division was questioned nearly from the start (e.g., Pietruszka, 1986), although it found support in studies based on small samples (Pietruszka, 1986; McLaughlin, 1989). Recently, Perry (1999) showed that

foraging behaviors span the entire range, from very sedentary to highly active. Iguanid lizards are often less active than autarchoglossans (Perry, 1999), but nonetheless show a range of behaviors, even within Phrynosomatidae (Figs. 10, 11). Huey and Pianka (1981) and Vitt and Price (1982) presented a set of hypotheses regarding correlations between lizard foraging mode and morphology, locomotor physiology, predation intensity, reproduction, and diet. They, and later workers (e.g., Magnusson et al., 1985; Vitt, 1990) suggested the existence of complex suites of traits, such that, for example, actively foraging species should have relatively high endurance, a streamlined morphology, and low reproductive output.

Physiological limitations can also affect sexual selection (Halliday, 1987). For example, females may prefer males with larger home ranges, perhaps because of greater resource availability. Reproductive success should then be correlated with the ability of a male to patrol his territory on a regular basis, and thus home range size. Similarly, lizard courtship behavior often involves the male following the female for large distances (e.g., Case, 1979), and males that show greater perseverance may be more likely to mate. In both examples, endurance is likely to be the key locomotor trait affecting the ability of the animal to cover distances. The time scale involved could be short (daily movement distance, DMD) or over weeks or months (home range size, HR). Indeed, endurance is positively correlated with DMD (Hertz et al., 1988; Garland, 1999). Because this aspect has already been studied, and because such data are highly time-consuming to record (Garland, 1983, 1993; Hertz et al., 1988), we will not emphasize DMD in the current study. The relationship between HR and locomotor abilities has never been investigated for any group of animals, and we propose to do so for the first time. We hypothesize that endurance capacity will be positively correlated with home range size. Preliminary (non-phylogenetic) analysis of available data (Perry et al., in prep.; Fig. 11) indicates a positive relationship in phrynosomatids, and also that *Phrynosoma* tend to have large home ranges (with the exception of *P. solare*, Baharav, 1975).

Although support now exists for some of the hypotheses listed above (e.g., Bennett et al., 1984; Magnusson et al., 1985; Garland, 1999), most are yet to be appropriately tested (Perry and Pianka, 1997). For example, early work indicated that relatively sedentary versus active-foraging lacertids differed in their locomotor performance (Huey et al., 1984), but updated phylogenetic information indicates this is not the case for those particular species (Perry, 1999). More generally, the complexities of behavior under natural conditions could make for weak connections between performance abilities and field behavior. Although generalizations are impossible at this juncture, several studies indicate that lizards may often employ speeds that are lower than those sustainable over the long term. Whether this is attributable to limitations imposed by the preferred habitat or for other reasons, and whether “preferred” speeds exist, are open and particularly interesting questions (Pennycuick, 1975; Bennett and Gleeson, 1979; Perry et al., 1988; Losos and Sinervo, 1989; Irschick and Losos, 1999; Autumn et al., 1999).

C. 4. PROPOSED RESEARCH

1. Study Species, Populations, and Phylogeny. To conserve effort and maximize productivity, we will build on data already available, often as a result of the previous award, and follow the advice of past reviewers in emphasizing the Phrynosomatidae. This monophyletic family contains three subclades (Fig. 1). Our results to date (Figs. 2-11) indicate it contains ample variation in locomotor and behavioral traits (see also Garland, 1994a; Miles, 1994a; Bonine and Garland, 1999; Irschick and Jayne, 1999; Perry, 1999; Perry et al., in preparation). All species that are largely terrestrial and occur primarily in arid or semi-arid habitats. All chosen species are diurnal and primarily insectivorous (Stebbins, 1985; Conant and Collins, 1991), though *Dipsosaurus dorsalis* is primarily herbivorous as an adult. We have considerable experience with nearly all of these species and know that they are amenable to the proposed measurements. We have also demonstrated ability to access sites in which all are found and obtain the necessary permits for their study and collection. For the main body of this work, we will therefore **focus on 17 species**, a subset of the 29 that we sampled previously (see section C. 1. and Figs. 2-11). Because populations may differ in physiological characteristics (Garland and Adolph, 1991), each species will be collected from a restricted geographic area. Most field work will be conducted at four field stations: Cedar Point (Nebraska), Deep Canyon and Granite Mountains (California), and Southwestern Research Station (Arizona). The differences

among species (see Background, and Garland, 1994a; Bonine and Garland, 1999) appear much greater than could be caused by environmental effects, including exercise training (e.g., Gleeson, 1979; Bennett and John-Alder, 1984; Garland et al., 1987; Miller, 1993; Conley et al., 1995). Hence, and for logistical reasons, our comparisons will not involve animals raised under common garden conditions. We will sample as follows (we allow some flexibility in case a particular population is low in numbers in a given year):

1. **Sand lizards** primarily inhabit open, sandy desert (e.g., Norris, 1958; Carothers, 1986; de Queiroz, 1992; Howland, 1992; Bulova, 1994; Jayne and Ellis, 1998). We shall study **four** species, representing all four genera in this group, for which partial data already exist: *Callisaurus draconoides*, *Cophosaurus texanus*, *Holbrookia maculata*, and *Uma notata* or *U. scoparia*.
2. **Horned lizards** (14 species of *Phrynosoma*) form the sister group to sand lizards, but nonetheless exhibit remarkable differences in general ecology and locomotor traits (Norris, 1958; Sherbrooke, 1981; Dial, 1986; Middendorf and Sherbrooke, 1992; Bulova, 1994; Perry, 1999; **Figs. 2, 3, 4, 6, 7**). We will study **four** of the following: *P. asio*, *P. cornutum*, *P. douglassii*, *P. mcallii*, *P. modestum*, *P. platyrhinos*.
3. The sister lineage to the previous two clades is the **Sceloporus group**. We will sample *Uta stansburiana* and 3 of the following 4 *Sceloporus*: *S. magister*, *S. occidentalis*, *S. undulatus*, *S. virgatus*.
4. To allow enhanced inference about ancestral values and subsequent directionalities of character evolution (e.g., see Zani, 1996), and to explore the phylogenetic generality of our results, we will also include **five outgroup species** which are reasonably similar to phrynosomatids in terms of body size and ecology (see **Fig. 1** for their relatedness to Phrynosomatidae). (1) *Crotaphytus collaris* is a predator that occurs in microsympatry with many phrynosomatids, and often feeds on them (Pianka, 1986; Stebbins, 1985) (*Gambelia wislizenii* will serve as a closely-related backup). (2) *Dipsosaurus dorsalis* is the only iguanid found in the U.S. and is extremely well studied in terms of physiological ecology (e.g., Norris, 1953; Mautz and Nagy, 1987), locomotion (e.g., John-Alder, 1983; John-Alder and Bennett, 1981; Gleeson and Harrison, 1988; Jayne et al., 1990; Irschick and Jayne, 2000), and muscle fiber-type composition and contractile properties (e.g., Gleeson et al., 1980; Putnam et al., 1980; Marsh, 1988). Its field locomotor behavior is unstudied. (3) *Laudakia stellio* (family Agamidae), like many members of the *Agama* group from which it was recently split, are ecologically and morphologically convergent with *Sceloporus* (Harris, 1963; Werner, 1966). (4) one species from each of two, typically more active families (Anderson and Karasov, 1981; Cooper, 1995; Perry, 1999) in the Autarchoglossa: Teiidae (*Cnemidophorus tigris*) and Lacertidae (*Podarcis sicula*).

Our understanding of lizard phylogeny is still evolving, though the relationships of the 17 focus species, and especially the 12 phrynosomatids indicated, are well known (**Fig. 1**). The general phylogeny for phrynosomatids, including the topology within sand lizards and the *Sceloporus* group, is well supported (Montanucci, 1987; Frost and Etheridge, 1989; de Queiroz, 1992; Wiens, 1993; Reeder and Wiens, 1996; Changchien, 1996; Macey et al., 1997; Wiens and Reeder, 1997; Schulte et al., 1998). The topology for all outgroups is drawn from the relationships identified by Arnold (Arnold, 1973, 1989a,b, 1997; Harris and Arnold, 1999; Harris et al., 1999), Estes et al. (1988), Fu (1998), Macey et al. (1997), Presch (1974), and Schulte et al. (1998). We will keep following developments in the field, and incorporate changes to this scheme as they emerge before conducting phylogenetic analyses.

2. Broad-based Correlational Study. Although gathering all data ourselves from the same populations would be optimal, this limits the number of species for which data can be collected. Hence, we will expand our study by using literature or additional species for both locomotor performance and field behavior. This also allows us to include field traits that are too time consuming to measure, such as home range size.

Data will be obtained through a literature survey, encompassing both reviews (e.g., Garland, 1993, 1999; Perry, 1999; Perry et al., in preparation; and see C. 3. Background) and primary literature (e.g., Losos, 1990; Bonine and Garland, 1999; Irschick and Losos, 1999). Given the multiple sources of information, sample sizes and phylogenetic representation will vary from comparison to comparison. However, preliminary examination of the database we have been assembling for home range size (Perry et al., in preparation) is promising. For example, the overlap between datasets for home range (drawn from

Perry et al., in preparation, e.g., see Fig. 11) and endurance (from Garland [1994a] and the previous award [see Fig. 3]) encompasses over 20 species in multiple families. We expect that other performance-behavior datasets will also include a large amount of overlap, thus allowing profitable analyses. All four field stations to be used have facilities for utilizing racetracks and treadmills, and we will also opportunistically gather additional data on locomotor speed and endurance using our previous techniques (Garland, 1994a; Bonine and Garland, 1999). For example, multiple data exist for such species as *Mesalina guttulata* (a lacertid found in Israel). A small investment in time, at locations already targeted for work because they host species listed in the previous section, will thus greatly enhance our ability to conduct simultaneous analyses of multiple traits and provide data on new species. Ultimately, we will be able to achieve wide phylogenetic coverage and a statistically meaningful sample for studying Performance → Behavior.

3. Morphology → Performance.

A. Muscle Contractile Properties. As in our previous work on fiber-type composition, we will study the iliofibularis (IF) muscle (diagram in fig. 1 of Putnam et al., 1980). Hence, we will eventually be able to correlate fiber-type composition (existing and in progress), enzyme activities (to be done on existing tissue, by Dr. T. T. Gleeson), and *in vitro* contractile properties. Although the PI has collaborated previously contractile studies (Bennett et al., 1989; Zhan et al., 1999), his lab is not equipped to do this work. Therefore, they will be done at the Univ. of Calif.-Irvine, in collaboration with Drs. R. K. Josephson and A. F. Bennett (see attached letters in Section I). Sample size will be 6 individuals/species.

The IF is a parallel-fibered muscle that spans both the knee and hip joints and is important in crural flexion and femoral retraction at the beginning of the propulsive stroke in lizards (Snyder, 1954; Jayne et al., 1990). In most species, the IF contains discreet red and white regions. In *Varanus exanthematicus*, electromyographic studies show that the red region is active at both low and high locomotor speeds, with regular bursts of activity, whereas the white region is active only above some threshold speed and with often irregular activity (Jayne et al., 1990). We propose to make two sets of contractile measurements, one on intact IF muscle and the other on fibers from the white, fast-glycolytic region only. (The red region has been studied separately in *Dipsosaurus dorsalis* [Gleeson et al., 1980], but it cannot be reliably recognized for dissection in all species [T. T. Gleeson, pers. comm.]) The IF has been used extensively in studies of lizard contractile properties (e.g., Putnam and Bennett, 1982; Marsh and Bennett, 1985, 1986; Gleeson and Johnston, 1987; Marsh, 1988; Johnson et al., 1993; Swoap et al., 1993), as well as histochemistry (Gleeson et al., 1980; Gleeson, 1983; Gleeson and Harrison, 1986; Mutungi, 1990; our own work), so we can employ well-established techniques and rely on a strong background when interpreting our results.

General protocols for contractile work follow Swoap et al. (1993) and Johnson et al. (1993), who studied *Dipsosaurus dorsalis*, one of our outgroup taxa. Following euthanasia, the iliofibularis will be isolated as described in Marsh and Bennett (1985; see also Gleeson et al., 1980). The red region and any damaged white fibers will be removed, leaving a mass of white (fast glycolytic) fibers. We will attempt to make this mass of similar size in all species by using a smaller cross-section of the white region from larger-bodied species. The left muscle will be used immediately, while the intact right muscle is maintained for up to 4 hours at room temperature (see Marsh and Bennett, 1985; Swoap et al., 1983) in oxygenated Ringer (composition in Swoap et al., 1993; pH maintained at approximately 7.5 by bubbling with 95% O₂:5% CO₂). The pelvis will be anchored to a hook attached to a force transducer constructed of silicon strain gauges (Entran Sensors Inc., Fairfield, NJ). The transducer is mounted in the base of plexiglas chamber containing circulating oxygenated Ringer at appropriate temperature (35-40°C, depending on species). The distal tendon is connected to a Cambridge Instruments model 300H ergometer, which is used to change muscle length. Force and length signals are amplified and displayed on a digital oscilloscope.

Muscle stimulation (Grass S48 stimulator, custom amplifier) is via platinum electrodes placed on either side of the muscle. Muscle length and stimulus strength are first adjusted to achieve maximal isometric tension in a tetanus (P_0), and muscle length (L_0) is then measured in place. Stimulation regimens will be adjusted for each species and frequency during tetanic contractions will be sufficient to maintain a smooth tetanus, but low enough to prevent decline in tension during the plateau phase (Marsh and Bennett,

1985). Isometric contractions are recorded within 1 s before and after a tetanus. Isotonic contractions are recorded using tetanic stimulation. 10-min rest periods are used between successive tetanic contractions.

The following standard isometric contractile properties will be recorded: P_0 , maximal isometric tension; P_t , peak twitch force (maximal twitch force); dP_0/dt , maximal rate of force development during a tetanus; dP_t/dt maximal rate of force development during a twitch; **TPT**, time to peak twitch force; **1/2RT**, time from peak twitch force to half-relaxation. Isotonic series will yield estimates of V_{max} , shortening velocity predicted at zero force, and W_{max} , maximal power output. Finally, following studies of our selected lines of house mice (Zhan et al., 1999), we will make a measurement of muscle **endurance** under isotonic conditions, assessed at a load corresponding to W_{max} . Repetitive shortening contractions will be induced by stimulation at 100 Hz (or as adjusted) in trains of 350-ms duration each second. Isotonic endurance is defined as the time required for W_{max} to decline to zero (i.e., time when muscle has lost ability to shorten). Although this has not been used in lizards, we were able to show significant training increases in mice given 8 weeks of wheel access (Zhan et al., 1999; shifts from approximately 8-11 sec in sedentary mice to 17-21 sec in trained individuals). We recognize that muscle fatigue under these conditions could be related to oxygen diffusion limitation, and will attempt to reduce this possibility by using a consistently small bundle of white fibers and by performing preliminary experiments on whole IF muscles for a size range of species. The muscle will be removed, the pelvis, tendon, and any damaged fibers dissected away, and the muscle weighed to the nearest 0.1 mg. Cross-sectional area will be calculated as mass/length.

The foregoing protocol will then be repeated for the right IF muscle, except that the muscle will be left intact (as in Putnam and Bennett, 1982). Stimulation regimen will be adjusted as necessary. We recognize that contractile properties of the whole IF will reflect a combination of the properties of the three different fiber types (FG, FOG, SO), and that we may observe bi- or tri-phasic curves. Nevertheless, an argument can be made that the whole-muscle *in vitro* preparation is more reflective of the workings of the muscle in the intact organism. Indeed, most studies of vertebrate muscle contraction have used whole muscles of mixed fiber-type composition. Moreover, our existing muscle fiber-type compositional data are for the whole IF. In any case, we will be able to cross-correlate values from the whole and white-only IF experiments, as well as determine empirically which better predicts whole-animal locomotor abilities.

With so many candidate independent variables, one risks finding spurious predictors of whole-animal performance. However, we expect muscle traits to be intercorrelated. For example, in a principal components analysis of individual variation in a salamander, Bennett et al. (1989) found evidence for three sets of traits that were internally intercorrelated but uncorrelated across sets: (P_0 , P_t , dP_0/dt , dP_t/dt), (TPT, 1/2RT), and (V_{max} , W_{max}). Based on first-principles of muscle function, these are not necessarily the exact groupings that one might have expected. In any case, we also expect to find sets of intercorrelated variables in the cross-species lizard data and will, therefore, use PCA to reduce dimensionality of the muscle variables into a smaller set of 2-3 PC scores, and use these scores in multiple regression and path analysis.

Although we will collaborate with one of its originators, we are not proposing to use the work-loop technique (see Josephson, 1985, 1989). Instead, we propose to use the above-listed "classical" measures of *in vitro* muscle performance. We believe this is appropriate because ours would be the first quantitative comparison of locomotor performance and muscle function across multiple species for any group of animals. In addition, estimates of power output derived from work loops should, in principle, be predictable from the other measures that we will make (e.g., see Josephson, 1993, 1999; James et al., 1996).

B. Muscle Enzyme Activities. Using frozen muscle tissues obtained under the previous grant, Dr. Todd T. Gleeson will measure citrate synthase, pyruvate kinase, and myofibrillar ATPase activity (see attached letter of collaboration in Section I). This was a subsidiary goal of the previous grant, and Dr. Gleeson is now offering to complete the work at minimal cost to the present proposal (supplies only).

C. Organ Masses and Hematocrit. As in our previous work, we will measure hematocrit (a simple indicator of blood oxygen carrying capacity) and also weigh the heart and liver of all animals sacrificed for muscle work. Thus, we will have these data for all 17 focal species. Literature provides data for almost 50 additional species (Pough, 1979, 1980; Seymour, 1987, 1989; Garland, 1993; Sutherland et al., in prep.).

4. Performance → Behavior. Although locomotion is an important part of many field behaviors, and although the relationship of many of those with performance abilities remains unexplored, it is impossible to address all of them here. Based on preliminary analyses and a priori hypotheses, we have chosen six metrics that encompass three different ways of assessing field locomotor behavior. **A.** Foraging is ubiquitous and involves locomotion in both searching for and capturing prey. **B.** The speeds at which animals move can be related to prey capture, predator escape, mate acquisition, and other facets of behavior. **C.** Home range size may indicate long-term, integrated locomotor effort. For each of the indices we measure, sample sizes will be >20 adult males per species (males were used in the previous research and will be used for muscle contractile work); home range data will be taken from the literature (Perry et al., in prep.) All of these data will be related to laboratory data on maximum speed and endurance.

A. Foraging Behavior. The numerical methods used to characterize lizard locomotion in the context of feeding were first proposed by Pianka et al. (1979; and see Huey and Pianka, 1981; Perry, 1995), and became standard (e.g., Anderson and Karasov, 1981; Perry et al., 1982; Magnusson et al., 1985; Pietruszka, 1986; McLaughlin, 1989; Cooper and Guillette, 1991; Perry, 1995, 1996, 1999; Werner et al., 1997; Eifler and Eifler, 1999) following the work of Huey and Pianka (1981). These methods involve recording of behavior in the field and attempting to exclude all locomotion not associated with food acquisition. However, as animals often multi-task, the measures produced may not purely reflect foraging behaviors, leading Perry (1999) to suggest that the term “time allocation” may be more appropriate. We use behavioral focal sampling (e.g., Moermond, 1979b) to select individuals for study, and each is only observed once. To avoid confounding with other behaviors, data obtained from animals interacting with conspecifics or predators (or obviously the observer) are omitted from the analyses, as are individuals that display behaviors intended primarily for thermoregulation. These precautions reduce the impact of non-foraging behaviors, but, as many observations are omitted, greatly increase data collection time. Regardless of the most appropriate terminology, these methods concentrate on describing movements that are mainly in the context of food acquisition. Thus, we expect a positive correlation to exist between endurance in the laboratory and the two indices derived from the observations of free-ranging animals, the number of moves made per minute (**MPM**) and the percentage of the time spent moving (**PTM**).

B. Velocity. More generally, several workers have reported lizard movement speeds in nature (e.g., Case, 1979; Moermond, 1979a; Pianka et al., 1979; Huey and Pianka, 1981; Magnusson et al., 1985; Vitt et al., 1993, 1995; Irschick and Losos, 1998), and Garland (1993) summarized the then-available, fragmentary data for almost 50 species. No attempt to relate such data to locomotor performance abilities has yet been made. We will use three metrics. Two, **overall mean velocity** and **actual speed while moving** (which excludes non-moving time), are well established (above refs.) and gauge average locomotor effort. These are predicted to correlate with endurance capacity. One new metric, the **90th percentile speed**, is added to indicate the effort involved in more rapid and less frequent movements; this should be more appropriate for comparison with maximal sprint speeds measured in the laboratory. To measure these indices, we will follow Irschick and Losos (1999) and videotape field-active lizards using a Mini-DV video camera with optical zoom lens (12X, which can be doubled with a tele-converter lens) for behavioral focal sampling (e.g., Moermond, 1979b). Similar methods, sometimes with incorporation of high-speed photography, have often been used to document the behavior of lizards both in the field (e.g., see Barry Sinervo's website: http://bionet.ucsc.edu/people/barrylab/public_html/lizardland/male_lizards.videos.html) and in the laboratory (e.g., Avery et al., 1987a,b; Irschick and Jayne, 1999). Similar to Irschick and Losos (1998) and Wilson and Franklin (2000), we will use videos to calculate speeds. Specifically, we will use a tape measure to record distance moved at the end of each observation, capture individuals and measure snout-vent length for scale, and use the number of frames to calculate duration of each move (only undisturbed lizards will be included). Observation length will vary, according to the frequency of movements typical of each species, to ensure that rare events are represented in our sample (e.g., Martin and Bateson, 1986). Active species, such as *Cnemidophorus*, will be observed for 15 minutes; most phrynosomatids for 30 min; individuals of especially sedentary species, such as *Phrynosoma modestum* (G.

Perry, unpublished data, and see Fig. 10), for 60 min each. We will calculate the mean values for each individual observed, and then use mean values for each species in our analyses.

C. Home Range (HR). Home range size is defined as the area traversed during the natural activities of food gathering, mating, and caring for young (Burt, 1943). Multiple factors determine the size of a lizard HR (Christian and Waldschmidt, 1984; Perry et al., in preparation; Stamps, 1977, 1983; Turner et al., 1969). However, as most of the HR area is often patrolled on a regular basis, we expect to see a positive correlation between laboratory-measured endurance and HR. No previous multi-species analysis of the relationship between laboratory locomotor performance and HR has been published. Because reliably measuring HR is beyond the modest time and manpower bounds we are proposing, we will rely on published studies, which we have compiled (Perry et al., in prep.; **Fig. 11**; C. 3. Background, and section 2 above), and this dataset currently stands at over 470 entries (each representing comprehensive information on males or females from a single population and study). Our database currently holds over 130 species, and data on endurance are available for over 20 of those. As opportunities arise during other work, we will collect endurance data for at least 10 more of these species, providing a more inclusive sample for analysis.

5. Phylogenetically Based Statistical Methods. Conventional statistical methods assume that data being analyzed represent independent observations drawn at random from the same underlying distribution. Interspecific comparative data often deviate from these assumptions because species descend from common ancestors, from which they inherit genomes, developmental programs, and often habitat occupancy (natal environment). For a given set of species, close relatives tend to resemble each other; consequently, conventional statistical methods are usually inappropriate for analysis of comparative data (e.g., Grafen, 1989; Harvey and Pagel, 1991; Garland et al., 1993; Martins, 1996c). Violation of statistical assumptions leads to invalid tests of hypotheses (e.g., inflated Type I error rates) and poor estimates of parameters.

We will emphasize Felsenstein's (1985) method of phylogenetically independent contrasts (IC), using the best topology available at the time and various types of arbitrary branch lengths, transformed as necessary. Recent work (Garland and Ives, 2000; Rohlf, manuscript) has shown that IC gives results that are fully equivalent to generalized least-squares approaches (e.g., Grafen, 1989; Martins and Hansen, 1997; Martins and Lamont, 1998). IC analyses are *not* highly dependent on the assumption of Brownian motion evolution (Díaz-Uriarte and Garland, 1996), and branch length errors generally do not have serious adverse effects on statistical performance (Díaz-Uriarte and Garland, 1998). Garland has extensive experience with its application to data similar to those we will obtain (e.g., Garland et al., 1991; Garland and Janis, 1993; Garland, 1994a; Garland and Adolph, 1994; Bauwens et al., 1995; Christian and Garland, 1996; Clobert et al., 1998; Bonine and Garland, 1999; Garland, 1999; Brashares et al., 2000). We will use the Phenotypic Diversity Analysis Programs (Garland et al., 1993, 1999; Garland and Ives, 2000), which are available from the PI on request. Moreover, a recent renewal NSF grant to Garland and co-PI Anthony R. Ives (DEB-9981967) will allow us to continue our work on developing and testing comparative methods and software, including the incorporation of measurement error (e.g., Martins and Lamont, 1998). For completeness and as recommended by various workers (e.g., Price, 1997; Garland et al., 1999), we will also present results of conventional statistical analyses (e.g., as in Bonine and Garland, 1999; Garland, 1999).

For description of allometric relationships and adjustments for body size, we will use least-squares regression and reduced major axis by independent contrasts. Relationships of performance to lower-level traits will be described and tested for statistical significance via correlation (with appropriate corrections to P values, e.g., Rice, 1989), partial correlation, regression, multiple regression, path analysis (Li, 1975; via LISREL, e.g., fig. 10.5 in Garland and Losos, 1994, and Bulova, 1994), canonical correlation, and principal components (for examples with lizard locomotion, see Garland, 1984, 1985, 1994a; Losos, 1990a,b; Miles, 1994a; Miles et al., 1995; Christian and Garland, 1996). We emphasize multivariate statistical analyses because they are most appropriate for our questions, and because they can lead to conclusions that differ from univariate or bivariate approaches (Willig et al., 1986; Corruccini, 1987; Willig and Owen, 1987).

17 species will yield adequate statistical power. Independent contrasts yield good power as compared with other methods (Martins and Garland, 1991; Martins, 1996b), especially when the phylogeny

is fully resolved (Purvis et al., 1994), as in the present case (Fig. 1). Our preliminary data show correlations that mostly exceed 0.6 (e.g., Bonine and Garland, 1999; Garland, 1999). Based on Garland and Adolph (1994, their fig. 5 and unpublished results), this is greater than the correlations of 0.5 or greater needed 1-tailed tests (appropriate for most of the relationships) to reach power of > 0.8 (Gill, 1991) with $\alpha = 0.05$.

C. 5. SIGNIFICANCE

Much of the theory underlying behavioral ecology incorporates the “phenotypic gambit” (Grafen, 1991), the assumption that individual behavioral traits (e.g., foraging mode) are free to evolve independently of other behavioral and lower-level morpho-physiological traits (e.g., muscle characteristics). This is an overly simplistic assumption, as many traits are functionally related. One consequence is that trade-offs may occur; for example, an increase in one trait may necessarily requires a reduction in the other. Another consequence is that, over evolutionary time, we may expect coadapted suites of traits to emerge, at levels ranging from the cellular to whole-organism function and behavior (Wagner and Schwenk, 2000).

Lizards exhibit an astounding diversity of locomotor behaviors and abilities, yet neither the mechanistic basis of interspecific variation in their locomotor performance, nor the adaptive significance of such variation, is well understood. Although the same could be said for other groups of organisms, lizards are an especially appropriate group in which to conduct integrative studies on this topic. They have often served as models in the study of vertebrate locomotion (Bennett, 1994; Garland and Losos, 1994; Gans et al., 1997), and an unusually extensive background literature concerning their locomotion is available. We will compare species of lizards to test the hypothesis that speed and endurance are negatively related, explore how their relationship is mediated by interactions of subordinate morpho-physiological traits, and test whether performance capacities can predict behavior in the field. As the lizards we will study retain the ancestral limb plan and are fairly generalized in terms of their locomotor modes, our findings should also provide a firm footing for future investigations of other groups, such as salamanders or terrestrial mammals.

Results from the present proposal would complement recent and ongoing studies of lizard locomotor biology. For example, two laboratories are continuing detailed work on the kinematics of locomotion in many of the same species that we will study (Reilly, 1998; Irschick and Jayne, 1998, 1999 [for videos of running lizards, see <http://www.biology.uc.edu/faculty/jayne/videos.htm>]). On another tack, Carrier (1991) has argued that lizard locomotor abilities may be constrained by the relationship between running and breathing (Wang et al., 1997). Consequently, lizard locomotion is often intermittent, and this may affect sustainable speed or endurance (Weinstein and Full, 2000) in unpredictable ways. If we find that endurance is *not* strongly related to muscle properties (e.g., see Bennett, 1994; our results to date), then future studies could examine cardiovascular and pulmonary factors, such as maximal heart rate or oxygen consumption (Garland, 1993; Thompson and Withers, 1997; Autumn et al., 1999) or pulmonary diffusing capacity (see Perry, 1989; Weibel, 2000). This would also lead logically to measurement of standard (resting) metabolic rate and hence tests of the aerobic capacity model for the evolution of activity capacity (Bennett and Ruben, 1979; Hayes and Garland, 1995; Dutenhoffer and Swanson, 1996). Costs of locomotion, which can have profound consequences for field behavior (Autumn et al., 1999), may be related to limb morphology (John-Alder et al., 1986), which varies greatly among phrynosomatids (Fig. 4; Irschick and Jayne, 1999). Information on field movements could eventually be used to estimate costs of locomotion as a fraction of the daily energy budget (Garland, 1983; Christian et al., 1997; Nagy et al., 1999). Finally, phrynosomatids show substantial variation in such traits as clutch size (Dunham and Miles, 1985; Pianka, 1986; Dunham et al., 1988; Clobert et al., 1998), thus allowing the possibility of future extensions to discover links with life history strategies. Indeed, several workers have posited the existence of complex adaptive suites in lizards, with *Phrynosoma* and *Cnemidophorus* -- two of our focal taxa -- viewed as showing extremes of coadaptation (Huey and Pianka, 1981; Vitt and Price, 1982; Magnusson et al., 1985; Pianka, 1986, 2000, pp. 100-103). In summary, our multidisciplinary study will greatly improve our understanding of the coadaptation and complex interactions of morphological, physiological, and behavioral traits related to locomotion, while also setting the stage for exciting future research.

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E. BIOGRAPHICAL SKETCHES

A. Theodore Garland, Jr. - P.I.

Department of Zoology, 430 Lincoln Drive,
University of Wisconsin-Madison
Madison, WI 53706
Office Phone: (608) 262-4437; Home Phone: (608) 278-7740
Fax: (608) 265-6320; Electronic Mail: tgarland@facstaff.wisc.edu
<http://www.wiscinfo.wisc.edu/zoology/faculty/fac/Garland/Garland.html>

a. Professional Preparation

University of Nevada, Las Vegas	B.S., Zoology (highest honors)	1974-78
University of Nevada, Las Vegas	M.S., Biology	1978-80
Universidad de Costa Rica	Org. for Tropical Studies Course	1981
University of Wollongong, Australia	Visiting Fulbright Scholar	1983-84
University of California, Irvine	Ph.D., Biological Sciences	1980-85
University of Washington	Postdoctoral Research Associate	1985-87

b. Appointments

1999-	Professor, Department of Zoology, University of Wisconsin-Madison
1996-97	Visiting Professor, Fac. Quimica, Bioquimica y Farmacia, U. of San Luis, Argentina
1995	Visiting Professor, Inst. Nac. Pesquisas da Amazonia, Dept. de Ecologia, Manaus, Brazil
1993-99	Associate Professor, Department of Zoology, University of Wisconsin-Madison
1993	Visiting Professor, Ecole Normale Superieure, Paris, Laboratoire D'Ecologie
1991-92	Assistant/Associate Program Director, Population Biology and Physiological Ecology Program, National Science Foundation
1990-	Affiliate: Conservation Biology and Sustainable Development Master's Program, University of Wisconsin-Madison
1988-	Affiliate: Biometry Master's Program, University of Wisconsin-Madison
1987-93	Assistant Professor, Department of Zoology, University of Wisconsin-Madison
1987	Lecturer, Department of Ecology and Evolutionary Biology, Univ. of California, Irvine
1986-87	Lecturer, Department of Zoology, University of Washington
1985	Visiting Scholar, Department of Biology, University of Chicago
1978-80	Assistant Curator, Vertebrate Museums, University of Nevada, Las Vegas
1978	Biological Technician, E.P.A Environ. Monitoring and Support Lab., Las Vegas, Nevada

c.i. 5 PUBLICATIONS MOST CLOSELY RELATED TO THE PROPOSED PROJECT

- Garland, T., Jr., and J. B. Losos. 1994. Ecological morphology of locomotor performance in squamate reptiles. Pages 240-302 in *Ecological Morphology: Integrative Organismal Biology*, P. C. Wainwright and S. M. Reilly, eds. University of Chicago Press, Chicago.
- Bauwens, D., T. Garland, Jr., A. M. Castilla, and R. Van Damme. 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioral covariation. *Evolution* 49:848-863.
- Clobert, J., T. Garland, Jr., and R. Barbault. 1998. The evolution of demographic tactics in lizards: a test of some hypotheses concerning life history evolution. *Journal of Evolutionary Biology* 11:329-364.
- Bonine, K. E., and T. Garland, Jr. 1999. Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. *Journal of Zoology, London* 248:255-265.
- Garland, T., Jr. 1999. Laboratory endurance capacity predicts variation in field locomotor behaviour among lizard species. *Animal Behaviour* 58:77-83.

BIOGRAPHICAL SKETCHES (continued)

B. Gad Perry - post-doctoral Research Associate
Department of Zoology, 430 Lincoln Drive,
University of Wisconsin - Madison
Madison, WI 53706
Office Phone: (608) 262-4437; Home Phone: (608) 255-6136
Fax: (608) 262-9083
Electronic Mail: gperry@facstaff.wisc.edu

a. Professional Preparation

Tel Aviv University	B.Sc., Biology	1984-87
Tel Aviv University	M.Sc., Zoology	1987-90
University of Texas, Austin	Ph.D., Zoology	1990-95
Ohio State University, Columbus	Postdoctoral Researcher, Zoology	1996-99
University of Wisconsin-Madison	Postdoctoral Researcher, Zoology	1999-

b. Appointments

1999-	Postdoctoral Researcher, University of Wisconsin-Madison
1996-99	Postdoctoral Researcher, Ohio State University, Columbus
1995	Lecturer, Department of Zoology, University of Texas, Austin
1990-95	Teaching Assistant/Assistant Instructor, Dept. of Zoology, University of Texas, Austin
1988-90	Consultant, Zoological Center Tel-Aviv Ramat-Gan, Israel
1987-90	Teaching Assistant, Department of Zoology, Tel Aviv University, Israel
1987-90	Curator of Herpetology, Department of Zoology, Tel Aviv University, Israel
1986-87	Biological Technician, Department of Zoology, Tel Aviv University, Israel

c.i. 5 PUBLICATIONS MOST CLOSELY RELATED TO THE PROPOSED PROJECT

Perry, G., I. Lampl, A. Lerner, D. Rothenstein, E. Shani, N. Sivan, and Y. L. Werner. 1990. Foraging mode in lacertid lizards: variation and correlates. *Amphibia-Reptilia* 11:373-384.

Perry, G. 1996. The evolution of sexual dimorphism in the lizard *Anolis polylepis* (Iguania): evidence from intraspecific variation in foraging behavior and diet. *Canadian Journal of Zoology* 74:1238-1245.

Perry, G., and E. R. Pianka. 1997. Foraging behaviour: past, present and future. *Trends in Ecology and Evolution* 12:360-364.

Werner, Y.L., S. Okada, H. Ota, G. Perry and S. Tokunaga. 1997. Varied and fluctuating foraging modes in nocturnal lizards of the family Gekkonidae. *Asiatic Herpetological Research* 7:153-165.

Perry, G. 1999. The evolution of search modes: ecological versus phylogenetic perspectives. *American Naturalist* 153:98-109.
<http://www.journals.uchicago.edu/AN/journal/issues/v153n1/970257/970257.html>

c.ii. 5 OTHER SIGNIFICANT PUBLICATIONS (of 37 total published or in press)

- Perry, G. and R. Dmi'el. 1994. Reproductive and population biology of the fringe-toed lizard, *Acanthodactylus scutellatus* in Israel. *Journal of Arid Environments* 27:257-263.
- Perry, G., G.H. Rodda, T.H. Fritts and T.R. Sharp. 1998. The lizard fauna of the islets surrounding Guam: island biogeography, phylogenetic history, and conservation implications. *Global Ecology and Biogeography* 7:353-365.
- Perry, G., R. Dmi'el and J. Lazell. 1999. Evaporative water loss in insular populations of the *Anolis cristatellus* group (Reptilia: Sauria) in the British Virgin Islands II: the effects of drought. *Biotropica* 31:337-343.
- Perry, G., R. Dmi'el and J. Lazell. 2000. Evaporative water loss in insular populations of *Anolis cristatellus* (Reptilia: Sauria) in the British Virgin Islands III: a common garden experiment. *Biotropica*. In press.
- Perry, G. Behavioral ecology. 2000 (trial edition now out, final edition in press). Open University Press, Tel Aviv (one of six study units comprising an animal behaviour course. In Hebrew).

d. Synergistic Activities

- 1999- Member, IUCN Invasive Species Specialist Group
- 1998-2000 Development of study units for Animal Behavior course, Open University, Israel
- Current Society Memberships: American Society of Naturalists, Asiatic Herpetological Society, Association for Tropical Biology, British Herpetological Society, Herpetological Association of Africa, Herpetologists' League, Societas Europaea Herpetologica, Society for Conservation Biology, Society for Ecological Restoration, Society for the Study of Amphibians and Reptiles, Zoological Society of Israel

e.i. ADDITIONAL COLLABORATORS (not listed above) WITHIN LAST 48 MONTHS

- College of Micronesia: Donald W. Buden
- Harvard University: Kate Jackson
- Ohio State University: Nancy A. Anderson, Brad E. Coupe, Thomas E. Hetherington
- Oregon State University: Leilani A. Leach
- University of Wisconsin-Madison: Kate R. LeVering
- U.S. Department of Agriculture: Earl W. Campbell, III
- U.S. Fish and Wildlife Service: John M. Morton, Michael Ritter

e.ii. GRADUATE AND POSTDOCTORAL ADVISORS

- Razi Dmi'el (M.Sc.)
- Eric R. Pianka (Ph.D.)
- Thomas E. Hetherington (Postdoctoral)
- Theodore Garland, Jr. (Postdoctoral)

e.iii. CURRENT AND FORMER GRADUATE STUDENTS AND POSTDOCS

None

F. BUDGET JUSTIFICATION

A. + B. Personnel

This project will take advantage of unique expertise offered by collaboration of five primary researchers and two graduate students. However, salary support is requested only for the Postdoctoral Research Associate (20 months) and one graduate student Research Assistant (6 summer months only). The PI, Theodore Garland, Jr., has expertise in measurement of lizard locomotor performance and in phylogenetically based statistical methods. His main contributions will be in coordination, scheduling, statistical analyses, writing, and synthetic activities.

The main body of work for this project will be shared by the Postdoctoral Research Associate, Gad Perry, and a graduate student, who will be named at a later date. Salaries for both are set by the University of Wisconsin. Perry has expertise in measurement of field locomotor behaviors. He will be in charge of (1) collecting all new field data and all new laboratory whole-animal performance data, (2) shipment of animals to the laboratory at U.C.-Irvine for measurement of muscle contractile properties, as well as (3) most of the literature search, non-phylogenetic data analyses, and writing. Requested funds will pay for his salary during both the field phase of this project (April-August 2001 and mid-April-July 2002) and the primary data analysis and writing periods (January-March 2001, September 2001-mid-April 2002, and August 2002). Perry is expected to start a faculty position by September of 2002, and work conducted thereafter under this project will be covered by his regular salary. Funds are thus requested to pay his salary from January 2001 through August 2002. It is also presumed that an unfunded extension may be implemented to finish writing.

Letters of collaboration from three senior researchers at other universities are attached at the end of this proposal in Section I. All of them will participate at no salary cost to this proposal. Muscle biochemistry on existing tissues will be conducted by Dr. Todd T. Gleeson (University of Colorado), who was co-PI on the previous award (see pages I-3 - I-4). Muscle contractile work will be done with Dr. Robert K. Josephson (see page I-1) and with assistance from Dr. Albert F. Bennett (see page I-2), both at the University of California-Irvine. The PI has known all three scientists for almost 20 years, and has previously co-authored with both Gleeson and Bennett.

The research will also provide a broad-based training opportunity for a graduate student who will primarily conduct the muscle contractile work at U.C.-Irvine, following training by, and under the supervision of, Drs. Josephson and Bennett. This work must be conducted on fresh tissue, and will consequently be carried out at the same time as Perry is conducting the field phase of this work. The student will spend six months in California, during the summers (June-August) of 2001 and 2002. The student will be in charge of analyzing this phase of the work, which is expected to form part of his/her dissertation. In addition, one of Garland's current graduate students, Ronald W. Sutherland, has just been awarded an NSF Graduate Research Fellowship to study adaptation in lizard blood oxygen carrying capacity and its relation to both locomotor abilities and field behavior. His work will likely emphasize within-population studies of various *Sceloporus* species, but he will potentially interact with many aspects of the work proposed herein. Hence, the Garland lab will contain a "critical mass" of workers in this general area for the next few years.

C. Fringe benefits.

Fringe benefit rates are set by the University of Wisconsin. As of January 2001, the proposed starting date, they will be 21% for the postdoctoral Research Associate and 13.5 % for the graduate student Research Assistant. Rates are assumed to increase by 1% as of July 2001 and by an additional 1% as of July 2002.

D. Equipment.

No items over \$5,000 are being requested.

E. Travel.

Funds are requested for travel to field study sites and to the laboratories of collaborators, as well as for attending meetings to disseminate findings.

i. Domestic travel. Most of the fieldwork will be carried out by Perry at four research stations: Cedar Point (Nebraska), Deep Canyon (California), Granite Mountains (California), and the South West Research Station (Arizona). All but two of the 17 primary species chosen will be studied at one of these, and additional data for the broad-based correlational study will be collected at them as opportunities arise. Based on current rates, coach air travel to domestic study sites is estimated at \$1,400 in year one and \$900 in year two. Based on communications from the directors of the four field stations to be used, fees at these sites (including dorm and laboratory space) are estimated at \$20/day in 2001 and slightly higher in 2002. Over the seven months Perry will spend at these stations during the study, total fees are estimated to total \$2,590 in year one and \$1,800 in year two. Car rental will be required for access to field sites. Based on currently available rates (for the state contract with National car company, about \$710/month in California and \$770/month in Arizona, for spring of 2001; 2002 rates are not available, but are assumed to be slightly higher), rental costs are estimated at \$3,000 in year one \$2,211 in year two. Gasoline for field work in the U.S. (\$600 total; \$400 year one, \$200 year two) is estimated as \$2/gallon, for 6,000 miles, at 20 miles per gallon.

The graduate student will be conducting his work at U.C.-Irvine. S/he will need to travel to the site during both years. In addition, Garland will travel to California and Colorado in year 2, to coordinate the final phases of the collaborative work there. The estimated total cost for this travel is \$600 in each of two years. The graduate student will spend a total of six months away from Madison. A per diem allowance of \$10/day is requested to cover the additional costs associated with out-of-town expenses, for a total of \$900 in each of two years.

Finally, \$2,400 (\$600 year one, \$1,800 year two) is requested to allow Garland, Perry, and the graduate student to attend 1-2 meetings each over the 2-year period of this award. Integrative projects of this type require interactions with a diversity of scientists, and meetings considered include the joint American Society for Ichthyology and Herpetology / Society for the Study of Reptiles and Amphibians / Herpetologists' League gathering, American Physiological Society, Animal Behaviour Society, International Congress of Herpetology, International Congress of Vertebrate Morphology, Society for Integrative and Comparative Biology, and Society for the Study of Evolution.

ii. International travel. One of the outgroups chosen for this study is the agamid, *Laudakia stellio*, which occurs in the Middle East, and which we intend to study in Israel. Relatively little information exists on agamid locomotor biology, making this an especially interesting outgroup for study. In addition, work in Israel towards the species targeted will include studies of two species of *Acanthodactylus*, lacertids which will serve as backups for *Podarcis sicula*. Additional species, of interest for the broad-based correlational study, will be studied during these trips. Specifically targeted are two species for which home range data exist (*Uromastix aegyptius* and *Mesalina guttulata*); other species will be studied opportunistically, in order to expand the phylogenetic foundation and geographical scope of this part of the study. \$2,900 is requested for airfare to allow two trips to Israel, one in 2001 and one in 2002. Although travel to this site is relatively expensive, the cost of work in Israel (\$1,930/month) is similar, overall, to that in the U.S. (\$1,700/month). This is because Perry will stay with relatives and utilize their resources, thus avoiding housing, car rental, and per diem expenses. Two trips are needed because unpredictable weather conditions make reliance on a single field season risky. Gasoline for field work in Israel (\$200 total; \$100 year one, \$100 year two) is estimated as \$6.5/gallon, for 600 miles, at 20 miles per gallon.

F. Participant support costs.

Not applicable.

G. Other direct costs.

i. Materials and supplies. The ergometer used for muscle contractile work will need to be refurbished (\$2,000). A Mini-DV video camera with optical zoom lens (at least X12), 2X teleconverter lens, and two additional 2-hour batteries will need to be purchased, for behavioral focal sampling, before work can start. The PI personally owns a Sony DCR TRV-900, which has excellent performance characteristics and a large user base (including several web sites). Cost of this or a similar model, including accessories, is estimated to be \$2,500. Other materials will include a laptop computer for data handling and analysis during Perry's 8.5 months in the field (\$2,500), software and updates for data handling and statistical analyses (\$500), storage media for both computer and video camera (all observations will be archived; each 1-hour mini-DV tape is currently approximately \$15, estimated total \$1,000), and chemicals and supplies for laboratory work conducted by our collaborators (\$1,000).

ii. Publication costs. Unfortunately, many journals now impose mandatory page charges, in addition to charging for production of reprints. To cover the production of papers, a total of \$2,000 (of which \$1,500 is slated for year 2) is requested for page charges, reprint costs, postage, and artwork for manuscripts. Dissemination of study abstracts and databases will be enhanced by use of the University of Wisconsin World Wide Web server, available to us at no extra cost.

iii. Other services. No funding requested.

iv. Subawards. No funding requested.

v. Other. For express mail service of live lizards from field sites to Irvine, California, \$200 per year is requested for each of the two study years. To cover other communication costs during field work (long distance phone and facsimile costs, e-mail service), \$200 per year is requested for each of the two study years.

G. CURRENT AND PENDING SUPPORT [as on NSF Form 1239 (10/99)]

Theodore Garland, Jr. - P.I.

All research located at the University of Wisconsin-Madison.

Current Support

"Morphological and Physiological Correlates of Locomotor Performance in Phrynosomatid Lizards"

NSF Ecological and Evolutionary Physiology Program

IBN-9723758

Award Amount: \$40,000 total costs

Period Covered: 15 August 1997 - 31 July 2000 (including 1-year no-cost extension)

Person-Months Committed: 1 calendar

"Responses to Artificial Selection for Voluntary Activity in House Mice"

NSF Animal Behavior Program and Ecological and Evolutionary Physiology Program

IBN-9728434

Award Amount: \$159,427 total costs

Period Covered: 1 June 1998 - 31 May 2001 (including 1-year no-cost extension)

Person-Months Committed: 1 calendar

"Phylogenetic Analyses of the Evolution of Continuous Characters"

NSF Systematic Biology Program

Award Amount: \$70,000 total costs

Period Covered: 1 April 2000 - 30 Sept. 2002

Person-Months Committed: 1 calendar

Pending Support

"Mice Selected for Hyperactivity as a Novel Model of ADHD"

NIH New Program Development proposal as part of the Waisman Center's core support grant,
which is titled "Wisconsin Center on Mental Retardation: Core Support"

Award Amount: \$144,000 total costs

Period Covered: 1 Aug. 2000 - 31 July 2002

Person-Months Committed: 1 calendar

"Morphological, Physiological, and Behavioral Correlates of Locomotor Performance in Phrynosomatid Lizards"

NSF Ecological and Evolutionary Physiology Program

This proposal. Will not be submitted to any other agencies.

Award Amount: \$127,537.50 total costs

Period Covered: 1 Jan. 2001 - 31 Dec. 2002

Person-Months Committed: 1 calendar

Submissions Planned in Near Future

None

H. FACILITIES, EQUIPMENT & OTHER RESOURCES [as on NSF Form 1363 (10/99)]

Theodore Garland, Jr. - P.I.

Garland is a Professor in the Department of Zoology at the University of Wisconsin-Madison. The Department of Zoology maintains and staffs full-service machine, electronic, and illustration shops, as well as some carpentry capabilities. Recharges are for materials and partial labor costs (\$3.00-5.00 per hour) only. Full secretarial service is provided at no charge. Approximately \$2,000 per year is provided to the P.I. for photocopying, supplies, and telephone costs.

Laboratory: The P.I. has approximately 1,300 square feet of lab/office space on the 4th floor of Birge Hall, with adjacent office space for 4-5 students or postdocs. Four separate wet lab rooms include two fume hoods, gas, air, and vacuum lines, hot, cold, and distilled water, and several sinks. Individual rooms are dedicated to (1) metabolic measurements, (2) measurement of speed and stamina, (3) measurement of other behaviors (e.g., open field, startle response), (4) dissection and biochemistry, and (5) computers.

Major equipment in the P.I.'s lab includes a dual-channel AMETEK Model S-3A oxygen analyzer, AMETEK Model CD-3A carbon dioxide analyzer, 9 mass-flow controllers (Sierra Instruments Model 844) for measurement of metabolic rate, Beckman DU-6 spectrophotometer, Thermomax (Molecular Devices Corp.) thermostated UV-Vis automated microplate reader, pH meter, two photocell-timed racetracks (one portable), four custom-built motorized treadmills (one portable), dissecting microscope, two microprocessor-controlled thermocouple temperature controllers, two microhematocrit centrifuges, and stand-up environmental chamber. Backup gas analyzers and spectrophotometers are available from other laboratories in the department. Access to two -80°C freezers is available for tissue storage; storage of carcasses is at -20°C in both a walk-in freezer and five chest-style freezers.

Computer: The P.I. has one 80286, one 80386, seven 80486, and two Pentium-based clone-PCs (running Microsoft DOS 6.2 and/or Windows 3.1 or 98), as well as Zenith SupersPort 286, NEC, IBM 755CE ThinkPad, and IBM 765D ThinkPad laptops, and one lonely MacIntosh that we use occasionally, mainly for file interchange. We also have an external tape backup. Three of the laptops are devoted to interfacing with oxygen and carbon dioxide analyzers, an automated microplate reader, and a portable electronic racetrack, all of which are in constant use for physiological and biochemical studies; the 80286 is permanently interfaced with behavioral testing equipment. Four of the 80486s are used periodically to automate running wheels for a mouse artificial selection experiment, but are otherwise available. A site license version of SAS is used for statistical analyses, along with the free R package (similar to S+). We also have PRELIS and LISREL (which we will use to implement path analysis, using maximum-likelihood model fitting techniques, e.g., fig. 10.5 in Garland and Losos, 1994; Bulova, 1994), BIOM-PC, NTSYS, Systat and Sygraph, SigmaPlot 4.0, PHYLIP, and MacClade. We have a university site license for the entire Microsoft Office suite, and we use WORD, Excel, and PowerPoint regularly. We also own Adobe Acrobat. We have two laserprinters and a color inkjet.

Animal: The Department of Zoology maintains two separate animal care facilities, one in the Zoology Research building and the other in Birge Hall. The P.I. is past chair of the departmental animal care committee, and was a member of the College of Letters and Science Animal Care and Use Committee. The P.I. has four rooms (approximately 180 square feet each) assigned in the secured 5th floor animal facility of Birge Hall, immediately above his lab space. Three rooms are used to house mice from an ongoing artificial selection experiment; another is used to house lizards. In addition, the P.I. has a walk-in environmental chamber on the 4th floor. The Department staff includes three full-time animal caretakers, and recharge rates are low in comparison with other institutions. Veterinary care is provided by the on-campus Research Animal Resources Center, with Lisa Krugner-Higby (D.V.M., Ph.D.) assigned to cover facilities in the College of Letters and Science.

Other:

Field stations. Most of the field work conducted under this proposal will be carried out at four established field stations. The main resource provided by these is the access to suitable populations of lizards. In addition, they offer:

- 1) The Southwest Research Station is located in southeastern Arizona and operated by the American Museum of Natural History. Facilities include residence halls, library, an outdoor aviary complex, an Animal Behavior Observatory, and laboratory including insect collection, herbarium, vertebrate collections, photography lab., microscopic facilities, constant temperature chambers, chemical hood, low-temperature freezer, precision balances, etc. For more information see <http://research.amnh.org/swrs/facility.html>
- 2) The Cedar Point Biological Station is located in western Nebraska and operated by the University of Nebraska - Lincoln. Facilities include lodgings and two research buildings, including wet and dry labs, 12 mesocosms (large tanks for aquatic experiments), a workshop, garage, parking area, and storage buildings. Additional information is available at <http://www.unl.edu/cedarpt/>
- 3) The Phillip Boyd Deep Canyon Desert Research Center is located in California Santa Rosa Mountains and operated by the University of California - Riverside. The station provides dormitory and laboratory space. For details see http://www.obfs.org/OBFS_Stations/CA_Boyd_Desert_Res._Cent..html
- 4) The Sweeney Granite Mountains Desert Research Center is located east of Barstow, California, and operated by the University of California - Riverside. The station provides dormitory and laboratory space. For details see http://www.obfs.org/OBFS_Stations/CA_Granite_Mt._Reserve_.html

Unpaid consultants. Several Madison faculty will serve as unpaid consultants. Dr. Catherine A. Marler (Psychology and Zoology) has considerable experience with field endocrinological studies of lizards (e.g., Marler and Moore, 1991). T. C. Moermond (Zoology) formerly worked extensively on lizard ecomorphology (e.g., Moermond, 1979a,b, 1986). Dr. K. L. Steudel (Zoology), is actively working on mammalian locomotor energetics and ecomorphology, and has published a series of studies on skeletal limb proportions of mammals in relation to the cost of locomotion and field behavior (e.g., Steudel and Beattie, 1993, 1995; Harris and Steudel, 1997).

Drs. John A. W. Kirsch and Robert E. Bleiweiss (both Zoology) are conducting molecular phylogenetic studies, primarily of mammals and birds, respectively. However, one of Kirsch's students has recently completed a DNA-hybridization study of North American lizards, emphasizing Phrynosomatidae (Changchien, 1996). Bleiweiss has been working on phylogenetically based statistical analyses of evolution and diversity in hummingbirds (e.g., Bleiweiss, 1997), and he and the P.I. consult regularly about such methods. Dr. J. R. Baylis (Zoology) is available to advise on general behavioral considerations and techniques. In the Department of Botany, Drs. T. J. Givnish and K. J. Sytsma have recently edited a volume on phylogenetic analyses of adaptive radiations (Givnish and Sytsma, 1997), and we have frequent discussions about these issues.

Drs. G. S. Mitchell (School of Veterinary Medicine; e.g., see Mitchell and Gleeson, 1985), H. V. Carey (School of Veterinary Medicine), W. P. Porter (Zoology), and W. H. Karasov (Wildlife Ecology and Zoology) will advise on general physiological techniques.

Advice on statistical analyses and software packages is available in the Division of Information Technology and in the Biometry Masters Program in the College of Agriculture and Life Sciences, of which Garland is a Faculty Affiliate. Garland's other major area of research is the development of phylogenetically based statistical methods, so statistical analyses of the present data are not seen as a major hurdle. For these studies, Garland collaborates with both Anthony R. Ives (Zoology; coauthor of Garland et al., 1992; Garland et al., 1999; Garland and Ives, 2000), co-PI on a separate NSF grant (DEB-9981967: "Phylogenetic Analyses of the Evolution of Continuous Characters") and Francois-Joseph Lapointe (University of Montreal; coauthor of Lapointe and Garland, in revision).