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The high degree of morphological similarity between cryptic species, populations which are morphologically nearly identical but reproductively isolated (Mayr, 1963), makes them model organisms for the investigation of ecological resource partitioning since the confounding effects of different body sizes can be greatly reduced. Often the morphological similarity of cryptic species is attributed to recent speciation; however, there are a variety of reasons besides recent speciation why taxa might be similar morphologically (reviewed in Larson, 1989). These include stabilizing selection on morphology (Sturmbauer and Meyer, 1992), convergence, or parallel evolution following speciation resulting from similar evolutionary pressures in different locations (Cody, 1969; Pianka, 1973; Charlesworth and Lande, 1982).

Similarity in morphology is often correlated with similarity in ecology (Cody, 1969; Pianka, 1973; Losos, 1990). The highly similar morphology of cryptic species might therefore result in their having similar ecological and physiological requirements. When found in sympatry, cryptic species are potentially competing for the same resources, such as preferred habitat or food type. Given this potential for intense competition, sympatric cryptic species might be expected to evolve differential use of resources (Patterson, 1992).

A recently discovered cryptic species complex of Pacific skinks is an excellent system with which to test hypotheses of resource partitioning between morphologically similar species. *Emoia cyanura* was thought to be the most common species of skink on the islands of the tropical Pacific for over a century (Brown, 1991; Ineich and

Zug, 1991) until it was shown to consist of two cryptic species, *E. cyanura* and *E. impar*, based on subtle morphological differences (Ineich and Zug, 1991). This morphological breakdown recently was corroborated by allozyme (Guillaume et al., 1994) and mitochondrial DNA (Bruna et al., 1995) analyses.

In addition to being nearly indistinguishable morphologically, there is also a parallel color polymorphism in both species. Although most individuals are dark and have three white dorsal stripes, "bronze" or "melanistic" individuals (juveniles as well as adults) are found in both species (Oliver and Shaw, 1953; Crombie and Steadman, 1986; Guillaume et al., 1994). They range in color from uniformly dark brown [in *E. impar* (Guillaume et al., 1994) and *E. cyanura* on Clipperton Island (Garman, 1899)] to *E. cyanura* that lack stripes below the head or are darkened by overall bronze body (Crombie and Steadman, 1986; Guillaume et al., 1994). Although the uniform, distinct, bronze coloration of *E. impar* individuals is probably a result of higher levels of melanin, bronze coloration in *E. cyanura* may be the result of increased melanin or the loss of stripe expression. Allozyme and mitochondrial DNA analyses have shown bronze individuals to be genetically identical to sympatric conspecifics (Guillaume et al., 1994; Bruna et al., 1996).

It is unknown whether *Emoia cyanura* and *E. impar* differ ecologically, because no studies investigating their use of resources have been conducted since their taxonomic revision. A posteriori analysis of voucher specimens by Ineich (1987) and Zug (1991) strongly suggested *E. cyanura* was found almost entirely in disturbed sunny areas, whereas *E. impar* was found predominantly in forested habitats. At least one author, however, has collected both species in the same microhabitat (Gill, 1993).

Given their morphological similarity, how do *E. cyanura* and *E. impar* coexist in sympatry? Prior to investigating any ecological differences between these species, we first quantified the level of morphological similarity between and within the populations of both species found on one island. Within this morphological framework, we tested the hypothesis that *E. cyanura* and *E. impar* are ecologically distinct. Most competing species of lizards segregate along one of three niche axes: habitat, food, or time of activity, in that order of importance (Schoener, 1974; Pianka, 1975; Toft, 1985). At least one study has found that skinks are opportunistic feeders showing little evidence of food niche partitioning (Auffenberg and Auffenberg,

1988); however, another has found that skinks can partition food resources quite finely (James, 1991). Temporal variation can be very difficult to assess because species can partition time of activity on both daily and seasonal scales (Toft, 1985). We therefore investigated the possibility of ecological segregation between these species by testing for partitioning along the most commonly varying niche axis: habitat. This was done by comparing the relative abundances of *E. cyanura* and *E. impar* in different habitat types on an island where they coexist.

Materials and methods.—Experiments were conducted in Rarotonga, Cook Islands (21°14'S, 159°47'W) from 14–29 Sept. 1994. Rarotonga, which is volcanic in origin, is the largest of the 15 islands which make up the Cook Islands group. It encompasses an area of 67 km², with its highest peak rising to a height of 653 m (Crombie and Steadman, 1986). The interior of the island is comprised of rugged mountains and valleys covered by pristine forest, whereas the outer coastal strip is flat, narrow, and primarily agricultural. Interior forest tree species include the Mato (*Homalium acuminatum*), Polynesian Chestnut (*Inocarpus fagifer*), Kavakava (*Pittosporum arborescens*), Kaiatea (*Weinmannia samoensis*), and the Asiatic Barringtonia (*Barringtonia asiatica*), as well as several species of fern. The lowlands are dominated by papaya (*Carica papaya*), taro (*Colocasia esculenta*), oranges (*Citrus cinensis*), coconuts (*Cocos nucifera*), and other crops, whereas the rocky beaches are bordered by strand vegetation such as Screw Pine (*Pandanus tectorius*), Beach Pea (*Vigna marina*), Scaveola (*Scaveola sericea*), and She-oak (*Casurina equisetifolia*) (McCormack and Künzlé, 1991).

A 1986 survey of Rarotonga's herpetofauna revealed the presence of five species of skink on the island as well as four species of gecko (Crombie and Steadman, 1986). While conducting this study and on a previous trip to the Cook Islands (Sept. 1989), we documented the presence of a fifth and sixth species of gecko: *Hemiphyllodactylus typus*, and *Hemidactylus frenatus* [the spread of *H. frenatus* throughout the Pacific has resulted in the displacement of several native species of gecko (Case et al., 1994) including some found on this island].

Predators of lizards on Rarotonga are found primarily in the lowlands. They include domestic cats (*Felis domesticus*), the Long-tailed Cuckoo (*Eudynamis taitensis*), Reef Heron (*Egretta sacra*), and the Indian mynah (*Acridotheres tris-*

tis)(Crombie and Steadman, 1986; McCormack and Künzle, 1991).

The following morphological measurements were recorded for 65 *E. cyanura* and 50 *E. impar* collected either by hand or in cardboard sticky traps (Wiles and Conry, 1990; Bauer and Sadlier, 1992) in Rarotonga, Cook Islands: (1) number of fourth toe and fourth finger subdigital lamellae, (2) number of fused and unfused middorsal scales, (3) relative anterior loreal scale length and height, (4) presence or absence of parietal eye, (5) underbelly color, (6) number of midbody scales, (7) number of upper and lower labial scales, and (8) left arm and leg length. These characters are traditionally used to differentiate between *Emoia* species (Brown, 1991), and four of these have been demonstrated to be diagnostic in distinguishing between *E. cyanura* and *E. impar* (characters 2–5; Ineich and Zug, 1991). We also recorded the snout–vent length (SVL) of each individual.

Variation between bronze and striped conspecifics as well as between species was compared using chi-squared (characters 3–5) and Mann Whitney U-tests (characters 1–2, 6–8). A *t*-test was used to compare the residuals of the regression of log(arm length) and log(leg length) vs log(SVL) to assess the relative differences in limb length between species after accounting for any possible differences in overall body length. Fifteen bronze *E. impar* and seven bronze *E. cyanura* were captured and used for statistical comparisons. Results were compared to published values for *E. cyanura* and *E. impar* (Zug, 1991). Individuals used for analysis are listed in Materials Examined.

To reliably identify these species, it is necessary to capture the animals first. Habitat segregation was inferred by capturing individuals in six transects of cardboard sticky traps placed at 15-m intervals (33 traps total). Transect locations are given in the Appendix. Microhabitat was described within a 1-m radius of each trap, and traps were checked for captures every 15 min for 2.5–3.5 h. Lizards were removed from traps by greasing them with mineral oil and pulling them away from the trap surface. All lizards were saved for morphological analyses. Each trap was located in one of five habitat types: (1) beach and adjacent strand vegetation and litter (Beach); (2) highly disturbed areas, pasture, trail edges, etc. (Disturbed); (3) stands of secondary growth (Secondary); (4) coastal groves of forest trees, with ground cover in these locations being a deep layer of broken coral covered with leaf litter (Coast Forest); and (5) primary forest in the interior of the island (Interior Forest).

A two-factor ANOVA was used to test for a species by habitat interaction. The catch per unit effort (total number of lizards caught per trap divided by the number of times the trap was checked) in different habitat types were compared using Mann Whitney U-tests. All trap capture information was pooled across transects of the same habitat type.

Results and discussion.—Bronze individuals did not differ significantly from their striped conspecifics with the exception of the following measurements: *Emoia impar*—number of upper labial scales ($P = 0.0542$) and fourth toe lamellae ($P = 0.0284$); *E. cyanura*—leg length ($P = 0.0282$). With the exception of these comparisons, bronze and striped individuals were combined for all other interspecific comparisons. A Bonferroni correction ($P = 0.05/\text{number of comparisons}$) was used to correct for multiple tests in these three cases. See Table 1 for a summary of all morphological measurements and statistical results.

Both species are relatively small and similar in size. The SVL of the *E. cyanura* individuals collected was $4.66 \text{ cm} \pm 0.64 \text{ SD}$ (range = 3.3–6.5 cm, $n = 70$); that of the *E. impar* collected was $4.35 \text{ cm} \pm 0.43 \text{ SD}$ (range = 2.9–5.0 cm, $n = 57$). *Emoia cyanura* and *E. impar* differ significantly in the number of fused middorsal scales ($P < 0.0001$), underbelly color, ($P < 0.0001$), presence or absence of parietal eye ($P < 0.0001$), the number of upper labial scales, ($P = 0.0293$), and anterior loreal scale shape ($P < 0.0001$). Bronze *E. cyanura* and *E. impar* differed in their leg length ($P = 0.0529$). When corrected for multiple tests, however ($P = 0.05/2$ results in a new $P = 0.025$), this result was not significant. All other comparisons were not significantly different. See Table 2 for a summary of all morphological measurements and statistical results.

The catch per unit effort of *E. cyanura* ranged from 0.06 ± 0.06 (mean number of individuals captured per trap each time checked \pm SE) in Interior Forest to 0.21 ± 0.07 in the Disturbed habitat type. The catch per unit effort for *E. impar* ranged from 0.05 ± 0.03 in the beach habitat to 0.19 ± 0.07 in Secondary habitat. A two-factor ANOVA indicated a significant habitat-by-species interaction ($P = 0.02$). The catch-per-unit effort of *E. cyanura* and *E. impar* differed significantly in habitat types Beach and Disturbed ($P = 0.01$ and $P = 0.02$, respectively) but not in habitat types Secondary, Coast Forest, and Interior Forest ($P = 0.82$, $P = 0.22$, and $P = 0.36$, respectively). A power analysis for *t*-tests (Zar, 1984) indicated a probability of

TABLE 1. COMPARISON OF BRONZE AND STRIPED *Emoia cyanura* AND *E. impar* FOR 11 MORPHOLOGICAL MEASUREMENTS. All values given are mean \pm 1 SE. (Ec = *Emoia cyanura*, Ei = *E. impar*, CNC = could not compute, MW-U = Mann Whitney U, Br = Bronze, Str = striped). Statistically significant values in bold.

Intraspecific morphological comparisons	Bronze Ec	Striped Ec	Range	Test	N (Br., Str.)	P-value
No. of 4th toe lamellae	60 \pm 4.4	64.73 \pm 3.99	55-71	MW-U	5, 35	0.9672
No. of 4th finger lamellae	42.8 \pm 1.24	42.75 \pm 4.01	34-50	MW-U	5, 36	0.6033
No. of middorsal scales	54.4 \pm 0.789	54.63 \pm 2.42	48-60	MW-U	5, 44	0.6164
No. of fused middorsal scales	0 \pm 0	0 \pm 0	0-0	MW-U	5, 44	>0.9999
No. of midbody scales	28.5 \pm 1.19	29.02 \pm 3.13	24-38	MW-U	5, 37	0.7842
No. of upper labial scales	7 \pm 0	7.04 \pm 0.42	6.0-8.0	MW-U	5, 41	0.7891
No. of lower labial scales	6.2 \pm 0.2	6.21 \pm 0.46	6.0-8.0	MW-U	5, 39	0.9341
Left arm length (cm)	1.68 \pm 0.08	1.48 \pm 0.22	1.0-1.8	MW-U	5, 42	0.0597
Left leg length (cm)	2.18 \pm 0.037	1.96 \pm 0.26	1.2-2.4	MW-U	5, 43	0.0282
Anterior loreal scale Height <,=,> Length	3, 0, 1	20, 7, 17		Chi-squared	4, 44	0.4756
Presence/absence of parietal eye	4, 1	44, 1		Chi-squared	5, 45	0.1918
	Bronze Ei	Striped Ei	Range	Test	N (Br., Str.)	P-value
No. of 4th toe lamellae	59.42 \pm 2.55	64.46 \pm 6.69	51-78	MW-U	11, 33	0.0284
No. of 4th finger lamellae	43.1 \pm 1.3	43.32 \pm 3.91	34-50	MW-U	9, 29	0.6666
No. of middorsal scales	54.46 \pm 1.08	54.41 \pm 3.33	48-61	MW-U	12, 37	0.9071
No. of fused middorsal scales	14.47 \pm 2.61	17.84 \pm 8.56	0-36	MW-U	12, 37	0.2214
No. of midbody scales	28 \pm 0.67	29.08 \pm 3.99	24-50	MW-U	10, 30	0.8492
No. of upper labial scales	6.58 \pm 0.52	6.85 \pm 0.42	6.0-8.0	MW-U	11, 35	0.0542
No. of lower labial scales	6.08 \pm 0.08	6.16 \pm 0.42	5.0-7.0	MW-U	11, 34	0.5305
Left arm length (cm)	1.47 \pm 0.09	1.4 \pm 0.18	1.0-1.7	MW-U	12, 37	0.9811
Left leg length (cm)	1.94 \pm 0.09	1.98 \pm 0.27	1.2-2.5	MW-U	12, 36	0.6831
Anterior loreal scale Height <,=,> Length	0, 0, 12	0, 3, 34		Chi-squared	12, 37	CNC
Presence/absence of parietal eye	1, 12	0, 37		Chi-squared	13, 37	0.2601

type II error of less than 10% for the nonsignificant results in the Secondary and Coast Forest habitats. Power analysis could not be conducted on the Interior Forest results, however, in part because of the small sample size relative to the pooled sample variance. See Figure 1 for all catch-per-unit effort results.

Emoia cyanura and *E. impar* are clearly very similar to each other morphologically. The *E. cyanura* and *E. impar* collected in Rarotonga did not differ from each other in any of the characters traditionally used to distinguish between *Emoia* species (lamellae, midbody scales, etc.) with the exception of the number of upper labial scales and those characters previously demonstrated to be diagnostic (underbelly color, fused middorsal scales, and presence or absence of the parietal eye; Ineich and Zug, 1991). As indicated in other studies, however, there was overlap in all three of the diagnostic characters suggesting proper identification requires the comparison of a suite of characters rather than

just one (Ineich and Zug, 1991). All morphological measurements were within the range documented by Zug (1991) for Fijian *E. cyanura* and *E. impar* (his table B), suggesting the morphological similarity of *E. cyanura* and *E. impar* is consistent in different Pacific island groups. Furthermore, all but three of the 21 morphological comparisons made between striped and bronze conspecifics were not significantly different, indicating that, with the exception of their unique coloration, melanistic individuals are also very similar morphologically to the other individuals of both species included in this study.

In light of their morphological similarity, it is not entirely surprising that these two species appear to be partitioning the habitat available to them. Although both species were found in all habitat types, beach and disturbed habitats had a significantly higher catch-per-unit effort of *E. cyanura* than *E. impar* (Fig 1). This trend was reversed in the less disturbed habitats sam-

TABLE 2. INTERSPECIFIC COMPARISONS OF 12 MORPHOLOGICAL MEASUREMENTS. All values are mean \pm 1 SE (Ec = *Emoia cyanura*, Ei = *E. impar*, MW-U = Mann Whitney U, SVL = snout-vent length, SD = standard deviation. Statistically significant results in bold.

Interspecific morphological comparisons	<i>E. cyanura</i>	<i>E. impar</i>	Test	N (Ec, Ei)	P-value
No. of 4th toe lamellae					
All Ec vs Striped Ei	64.73 \pm 0.64	66.36 \pm 1.30	MW-U	40, 33	0.2926
All Ec vs Bronze Ei	64.73 \pm 0.64	62.73 \pm 0.63	MW-U	40, 11	0.0731
No. of 4th finger lamellae					
No. of middorsal scales	42.75 \pm 4.01	43.32 \pm 3.91	MW-U	40, 38	0.5207
No. of fused middorsal scales	54.63 \pm 2.42	54.41 \pm 3.33	MW-U	49, 49	0.6501
No. of midbody scales	0 \pm 0	17.84 \pm 8.56	MW-U	49, 49	<0.0001
No. of upper labial scales	29.02 \pm 3.13	29.08 \pm 3.99	MW-U	42, 40	0.9925
No. of lower labial scales	7.04 \pm 0.42	6.85 \pm 0.42	MW-U	46, 46	0.0293
No. of upper labial scales	6.21 \pm .046	6.16 \pm 0.42	MW-U	44, 45	0.7546
Left arm length (cm)					
Left leg length (cm)	1.48 \pm 0.22	1.4 \pm 0.18	MW-U	47, 49	0.1822
All Ei vs Bronze Ec					
All Ei vs Striped Ec	2.18 \pm 0.04	1.98 \pm 0.04	MW-U	5, 48	0.0529
All Ei vs Striped Ec					
	1.94 \pm 0.04	1.98 \pm 0.04	MW-U	43, 48	0.4759
Anterior loreal scale Height					
<,=,> Length	23, 18, 7	0, 3, 46	Chi-squared	48, 49	<0.0001
Presence/absence of parietal eye					
Underbelly color (white, dusky, bronze)	48, 2	1, 49	Chi-squared	50, 50	<0.0001
SVL	44, 3, 0	0, 40, 9	Chi-squared	47, 49	<0.0001
Residual log (arm length) vs log (SVL)	4.66 \pm 0.64 SD	4.35 \pm 0.43 SD			
Residual log (leg length) vs log (SVL)			<i>t</i> -test	39, 49	0.3633
			<i>t</i> -test	48, 48	>0.9999

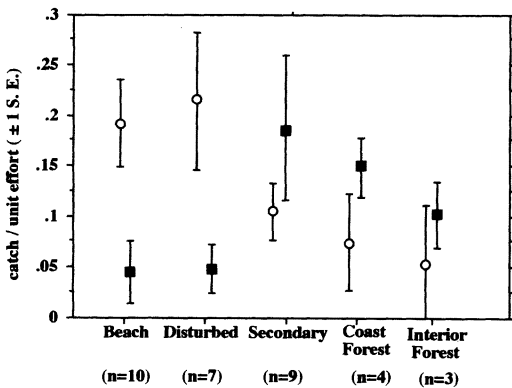


Figure 1

Fig. 1. Mean catch-per-unit effort \pm 1 SE of *Emoia cyanura* (open circles) and *E. impar* (filled squares) in five habitat types ranging from beach to full canopy forest (see text for details). Capture rates for *E. cyanura* were significantly higher in Beach and Disturbed habitats but not in the Secondary, Coastal Forest, or Interior Forest habitats.

pled. Although not significantly different, the catch-per-unit effort of *E. impar* was higher than that of *E. cyanura* in the Secondary, Coast Forest, and Interior Forest habitat types. Although the difference in habitat use is not as discrete as previously suggested (Ineich, 1987; Zug 1991), these results support the impressions implied in prior studies of habitat use in disturbed habitats.

Our results are similar to those of other scincid cryptic species complexes. *Lipinia noctua* and *L. rouxi*, two Pacific cryptic species, overlap entirely in the traditional characters used to differentiate between scincids. Nontraditional morphological characters (such as the absence of a left oviduct) and allozyme evidence clearly indicate the two are different species, however (Greer and Mys, 1987; Austin, 1995). *Leiopisma inconspicuum*, *L. maccanni*, and *L. nigriplantare polychroma* were until recently considered one subspecies (Patterson and Daugherty, 1990) based on their morphological similarity. An investigation of their microhabitat segregation found that each species was associated with a particular microhabitat (rock outcroppings,

grass tussocks, etc.) even when individuals of the various species were within a meter or two of each other (Patterson, 1992). As with *Emoia cyanura* and *E. impar*, the species are morphologically very similar (differing in color pattern), which suggests there are a variety of mechanisms exerting strong selective pressures which result in habitat segregation in lieu of morphological character displacement.

Competition may be one mechanism responsible for the observed distribution. First, if there were some preferred or limiting resource in the Beach and Disturbed areas, the difference in capture frequency in those habitat types could be the result of competitive exclusion of *E. impar* by *E. cyanura*. Second, the overlap in habitats Secondary, Coast Forest, and Interior Forest, could be the result of fewer competing species on Rarotonga than in the locations where *E. cyanura* and *E. impar* have been previously studied. The other skink species present on the island are either primarily arboreal (*E. trossula*), arboreal and secretive (*Lipinia noctua*), or are found mainly on the trunks of palm trees and piles of coral (*Cryptoblepharus* spp.). There are therefore no other terrestrial lizards that may be competing directly with *E. cyanura* and *E. impar* in Rarotonga. In archipelagos further west, such as Fiji, *E. cyanura* and *E. impar* are found in sympatry with other species of skinks (Zug, 1991), which could result in more extreme habitat segregation observed there.

An alternative hypothesis, however, is that *E. impar* is unable to tolerate the higher temperatures on the beach and open habitats, resulting in its capture at lower rates in those environments. The preferred body temperature of lizards is often within a narrow defined range determined by physiological requirements (Bennett, 1980; Huey, 1982; Adolph, 1990). This physiological range has been proposed as a factor limiting the microhabitat selection of different species (e.g., Adolph, 1990; Law and Bradley, 1990; Diaz, 1994). This may be the case on Rarotonga, with *E. cyanura* preferring warmer basking and foraging sites, whereas *E. impar*'s thermal optimum limits its foraging to the more shaded, darker habitats found in close canopied forests and coastal groves of *Barringtonia* and *Inocarpus fagifer*.

A thermal preference for different habitats could be the result of character displacement when the two species came into contact, or the two species may already have been ecologically distinct prior to their sympatry and ecological interaction. If the two species differ as a result of their contact, their habitat affinities may be

different on islands where they occur allopatrically, which could be determined by investigating habitat use on those islands. To determine whether their ecological differences have a historical basis (i.e., they were distinct prior to contact), one could determine whether they are closest relatives (Brooks and McLennan, 1991). If these species are sister taxa, their differences in habitat preference were clearly not inherited. It appears that *E. cyanura* and *E. impar* are not sister taxa (Bruna et al., 1996), suggesting that the mechanism responsible for their habitat affinities could be either historical or the result of character displacement resulting from contact, and therefore additional work comparing allopatric and sympatric populations is needed.

Finally, Williams (1969) suggested that more vagile invading species of Antillean *Anolis* could tolerate a wider range of physiological stresses and therefore displace resident species in marginal habitats. The observed segregation in habitat could be the result of invasion by a more vagile, generalist, *E. cyanura*, resulting in the displacement of *E. impar* from more disturbed habitats.

There were too few captures of melanistic individuals of either species to test for habitat segregation by color morph; however, as in the case of their striped conspecifics, bronze individuals were captured in all five habitat types. Although melanism is usually thought to be advantageous in darker, forested habitats for its thermoregulatory efficiency (Gibson and Falls, 1979; Andren and Nilsen, 1981), seven of 13 bronze *E. impar* captured were caught in the more sunny and open highly disturbed areas or along trails. A greater number of bronze *E. cyanura* were also captured in sunny areas than in forested areas, with six of nine being captured in beach strand vegetation. Since there are several examples of melanistic lizards found on small, hot, sparsely vegetated islands (see review in Censky and Paulson, 1992), however, a different selective mechanism, such as predation pressure (Kettlewell, 1955; Brown et al., 1991), may be responsible for the distribution of melanistic individuals in the various habitats.

In considering these results, it is essential to remember that, with the exception of the beach habitat, both species were captured in all habitat types. *Emoia cyanura* and *E. impar* are highly active lizards, moving constantly in search of prey and basking sites (Zug, 1991) between various habitat types. Future studies of this system may wish to consider the amount of time spent in each habitat type as an additional means of

assessing preferred habitat. Furthermore, it has recently been demonstrated that individuals currently recognized as *E. cyanura* and *E. impar* from different regions of the Pacific are genetically distinct from each other (Bruna et al., 1996), representing the potential presence of several other cryptic species. Considering the ecological relationships between these species in light of their phylogenetic history may yield much insight regarding the evolution of ecological segregation between morphologically similar taxa.

Materials examined.—Specimens used in this study are deposited at the California Academy of Sciences under CAS numbers 199867–199982.

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APPENDIX

Transect locations and number of traps of each habitat type present in each transect follows: (1) coastal stand of *Barringtonia asiatica* trees, north of the main road 1.5 km east of the Kii Kii motel (2 Coast Forest, 3 Secondary, and 1 Beach); (2) beach directly across from the Are-Renga Motel and Catholic Church in Arorangi (8 Beach); (3) mouth of the Paringaru stream, Muri Beach (1 Secondary, 2 Coast Forest, 3 Disturbed); (4) inland pastures and forest near the Sheraton Hotel, near the road to Wigmore's Waterfall (3 Disturbed, 2 Secondary); (5) One-roa Islet (1 Beach, 1 Secondary, 1 Interior Forest); and (6) Papua stream crossing of the Cross Island walk (2 Interior forest, 2 Secondary, 1 Disturbed).

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Reproductive Season, Clutch Size, and Egg Size of the Rainbow Darter, *Etheostoma caeruleum*, from the Homochitto River, Mississippi, with an Evaluation of Data from the Literature

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A major goal of life-history studies is to infer evolutionary causes of historical changes in the reproductive patterns of organisms. One common approach involves broad comparisons of traits across many species. For darters, such comparisons (Paine, 1990; Bart and Page, 1992) have been based on data drawn from a literature that largely consists of studies of only one species and often on only one population in a single year. Thus, interspecific comparisons must often assume that interspecific variation is sufficiently great relative to intraspecific variation to allow accurate comparisons.

There are two ways to incorporate intraspecific variation into interspecific comparisons. One is for researchers to emphasize multiyear and multipopulation studies addressing intraspecific and interspecific variation. The labor-intensive nature of such research will result in few studies, and those that are initiated will be slow in coming to fruition. An alternative ap-