mites as prey, however; one specimen contained 17 termite head capsules and no organic detritus. How such small insects would be detected and ingested singly remains unknown. Barbour and Loveridge (1928) reported that *Boulengerula boulengeri* from the Usambara Mountains, Tanzania, also fed on termites, and Wake (1980) reported them as prey of *Dermophis mexicanus*. Of the 50 stomachs of the semi-aquatic *Typhlonectes compressicaudus* examined by Moodie (1978), most were empty. The rest contained unidentified digested matter, one had been feeding on arthropods, and one contained four shrimp. Gut nematodes from *A. taitana* were identified by Loveridge (1936) as *Oxyuris* sp., and Ubelaker (1966) lists the nematodes *Pharyngodon boulengerula* and *Raillietnema loveridgei* from the closely related *Afrocaecilia uluguruensis*.

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LITERATURE CITED

BARBOUR, T., AND A. LOVERIDGE. 1928. A comparative study of the herpetological faunae of the Uluguru and Usambara Mountains, Tanganyika Territory, with descriptions of new species. Mem. Mus. Comp. Zool. 50:87–265.

BRECKENRIDGE, W. R., S. NATHANIEL, AND L. PEREIRA. 1987. Some aspects of the biology and development of *Ichthyophis glutinosus* (Amphibia: Gymnophiona). J. Zool., London 211:437–449.

DUELLMAN, W. E., AND L. TRUEB. 1986. Biology of Amphibians. McGraw-Hill, New York. 670 pp.

GUNDAPPA, K. R., T. A. BALAKRISHNA, AND K. SHAKUNTALA. 1981. Ecology of *Ichthyophis glutinosus* (Linn.) (Apoda, Amphibia). Curr. Sci. 50:480–483.

LOVERIDGE, A. 1936. Scientific results of an expedition to rain forest regions in eastern Africa. VII. Amphibians. Bull. Mus. Comp. Zool. 79:369–430.

MAINA, J. N., AND G. M. O. MALOIY. 1988. A scanning and electron microscopic study of the lung of a caecilian *Boulengerula taitanus*. J. Zool., London 215: 739–751.

MOODIE, G. E. E. 1978. Observations on the life history of the caecilian *Typhlonectes compressicaudus* (Dumeril and Bibron) in the Amazon Basin. Can. J. Zool. 56:1005–1008.

NUSSBAUM, R. A., AND M. WILKINSON. 1989. On the classification and phylogeny of caecilians (Amphibia: Gymnophiona), a critical review. Herp. Monogr. 3:1–42.

STEWART, M. M. 1967. The Amphibians of Malawi. State Univ. New York Press, Albany. 163 pp.

TAYLOR, E. H. 1968. The Caecilians of the World. A Taxonomic Review. Univ. Kansas Press, Lawrence. 848 pp.

UBELAKER, J. E. 1966. Additional records of parasites from caecilians (Amphibia: Apoda). J. Parasitol. 52: 431.

WAKE, M. H. 1980. Reproduction, growth, and population structure of the Central American caecilian *Dermophis mexicanus*. Herpetologica 36:244–256.

WOOD, S. C., R. E. WEBER, G. M. O. MALOIY, AND K. JOHANSEN. 1975. Oxygen uptake and blood respiratory properties of the caecilian *Boulenergula taitanus*. Resp. Physiol. 24:355–363.

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Relationship between Ovarian and Fat Body Weights during Vitellogenesis for Three Species of Lacertid Lizards

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Except for a few species with continuous or no seasonal reproductive activity, lizards exhibit lipid cycling associated with reproduction, winter dormancy or both (see Derickson, 1976a, for a review). Several European lacertid lizards show distinct fat body cycles peaking in late summer or early fall but as in many temperate zone lizards, fat stores are not depleted over winter but decline throughout the spring reproductive season (Braña, 1983; Argüello, 1990; Braña et al., 1990; Castilla and Bauwens, 1990). This pattern is similar in both sexes, although fat bodies of males are usually smaller than those of females (about one half in *Lacerta monticola* when maximally enlarged; Argüello, 1990; Braña et al., 1990) and their stores seem to be used to support behavioral activities associated with reproduction more than for gonadal recrudescence (Braña et al., 1990; Castilla and Bauwens, 1990). In females, on the contrary, the direct role of fat stores in egg development, particularly for the first vitellogenesis, has been clearly shown in the iguanid *Uta stansburiana* (Hahn and Tinkle, 1965), and this pattern seems to be widespread among temperate and tropical lizards (Jameson and Allison, 1976; Guillette and Casas-Andreu, 1981; Vitt and Goldberg, 1983; Vitt and Cooper, 1985; Etheridge et al., 1986; Guillette and Bearce, 1986). Thus, lipid stores appear to be a critical factor for reproductive success in reptiles living in areas with seasonal fluctuations in food availability, and data on the relationships between fat stores and gonadal development are necessary to understand reproductive strategies. In this paper we examine relationships between fat body and ovarian weight in three species of lacertid lizards during the reproductive season, mainly focusing on the first vitellogenesis.

A total of 40 adult females of *Podarcis bocagei* (snout-vent length, SVL, mm; mean ± 1 SE; 54.8 ± 0.6; range 49.1 to 60.6), 45 *P. muralis* (58.3 ± 0.5; 51.7–62.9), and 52 *Lacerta monticola* (62.4 ± 0.8; 54.3–72.6) were collected in central Asturias (northern Spain) for this study. *Podarcis bocagei* and *L. monticola* are endemic species with restricted distributions in the northwest of the Iberian Peninsula, whereas *P. muralis* occurs

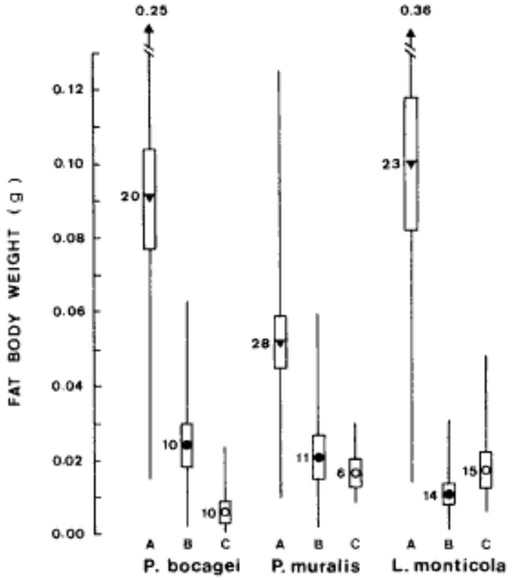

FIG. 1. Fat body weights (mean + 1 SE, and range; sample sizes are given in figures) of mature females of *Podarcis bocagei*, *P. muralis*, and *Lacerta monticola*, corresponding to the following situations: (A) Preovulatory females; from emergence to the first ovulation; (B) Females with oviductal eggs for the first clutch; (C) Females with vitellogenic follicles or oviductal eggs for later clutches.

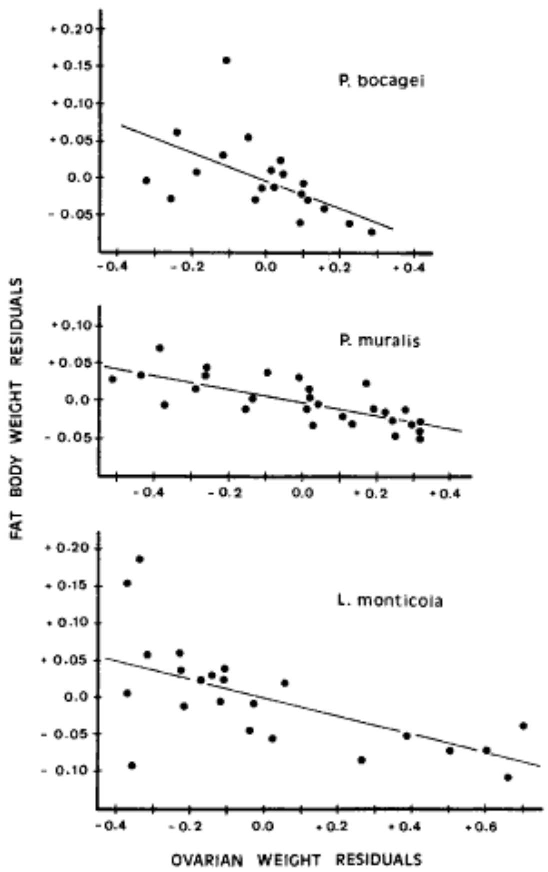

FIG. 2. Relationships between residuals of fat body weights and residuals of ovarian weights in females of *Podarcis bocagei*, *P. muralis*, and *Lacerta monticola* during the first vitellogenesis (from emergence to first ovulation). Residuals are from the regressions on female size or condition.

widely in southern Europe, including northern Spain (see Salvador, 1985). These species are small, diurnal lacertids whose reproductive season begins shortly after emergence (early March to middle April) and lasts until the middle of July. During the reproductive activity period females can lay up to three clutches under favorable conditions (Saint Girons and Duguy, 1970; Braña, 1983). Lizards were collected by hand and noose prior to first oviposition (late March to mid May) in 1983 for *P. bocagei*, and in 1984 for *P. muralis* and *L. monticola*. Additional specimens were caught to check for stomach contents and state of fat stores after the first oviposition (from mid May to mid July, 1983 and 1984). In addition to the information provided by tracking the cycle of the females in the field, the existence of previous clutches was confirmed by the presence of corpora lutea and enlarged oviducts. Specimens were cooled in the field and later etherized and examined within 24 h of capture. For each female, the following measurements were taken: SVL (to the nearest 0.1 mm); total body mass (0.01 g); ovary mass (and oviductal egg mass, if applicable, to the nearest 0.001 g); and fat body mass (0.001 g). Lipid stores were estimated by means of the mass of inguinal fat bodies, which represents an important fraction of total body lipids and has been frequently shown to fluctuate in a similar way (Cale and Gibbons, 1972; Jameson and Allison, 1976; Vitt and Cooper, 1985; Etheridge et al., 1986).

Fat bodies were not exhausted during winter, so their masses in preovulatory females at the onset of the activity period averaged 0.092 ± 0.014 (g; mean ± 1 SE) in *P. bocagei*, 0.052 ± 0.007 in *P. muralis*, and 0.106 ± 0.017 in *L. monticola*. These represented 2.85% ± 0.42, 1.26% ± 0.16, and 2.08% ± 0.31, respectively, of total female body mass. In all three species, fat bodies of females which had finished the first vitellogenesis were significantly smaller than those of females with enlarged vitellogenic follicles prior to the first ovulation (Fig. 1; one-way ANOVAs: $F_{2,37} = 15.40$, $P < 0.0001$ for *P. bocagei*; $F_{2,42} = 5.87$, $P < 0.01$ for *P. muralis*; $F_{2,49} = 14.98$, $P < 0.0001$ for *L. monticola*). However, no significant differences were found in fat body masses between females with first clutch oviductal eggs and those containing vitellogenic follicles or oviductal eggs for later clutches (Student-Newman-Keuls test, $P < 0.05$; see Fig. 1).

Relationships between fat body and ovarian masses for mature females of the three lizard species during the first vitellogenesis are shown in Fig. 2. In order to avoid confounding effects due to correlations of both fat body and ovarian masses with female size or condition, we computed residuals of the regressions on female SVL, mass (without ovaries and fat bodies), or condition (estimated by means of the residuals of

TABLE 1. Number of prey items per stomach for female lacertids caught during the first vitellogenesis (March and April), and later in the reproductive season (May to July).

	Prey per stomach						
	March–April			May–July			
	Mean	SD	N	Mean	SD	N	
Podarcis bocagei	1.86	0.35	23	3.89	1.12	17	*
Podarcis muralis	2.00	0.44	22	7.54	1.62	23	*
Lacerta monticola	4.39	0.71	18	9.90	2.41	34	*

* Differences between periods significant at $P < 0.001$.

the regression of logarithm of fat body masses on SVL). To obtain such residuals, we used as the predictor variable in each case that explaining the largest amount of variance of the dependent variable (ovarian or fat body mass). For *P. bocagei*, female SVL was the main predictor variable for ovarian mass ($r^2 = 0.630$; $P < 0.0001$) and female mass for fat body mass ($r^2 = 0.222$; $P = 0.036$); for females *P. muralis* ovarian mass increased with somatic mass ($r^2 = 0.185$; $P = 0.022$), whereas SVL explained the largest amount of variance in fat body mass ($r^2 = 0.316$; $P < 0.01$); for *L. monticola* the selected predictor variables were SVL for ovarian mass ($r^2 = 0.092$; $P = 0.159$) and condition for fat body mass ($r^2 = 0.270$; $P = 0.011$).

When effects of female size (SVL or mass) or condition were removed by using residuals of regressions, there were significant inverse relationships between ovarian and fat body masses in all three lizard species (Fig. 2; *P. bocagei*: Fat Body Mass = $6.2 \times 10^{-5} - 0.198$[Ovarian Mass]; $r^2 = 0.296$; $P < 0.05$; *P. muralis*: FBM = $7.9 \times 10^{-6} - 0.0088$ OM; $r^2 = 0.554$; $P < 0.001$; *L. monticola*: FBM = $7.5 \times 10^{-7} - 0.124$ OM; $r^2 = 0.348$; $P < 0.01$). Not surprisingly, slopes of the above regressions are higher in the species with higher fat body masses relative to female mass at the onset of vitellogenesis.

The reported relationship between fat body and ovarian masses in female lacertid lizards suggests that an important fraction of the energy allocated to follicle enlargement in early spring came from lipid stored in fat bodies, which agrees with previous findings in numerous reptilian species (Hahn and Tinkle, 1965; Derickson, 1976b; Congdon and Tinkle, 1982; Diller and Wallace, 1984; Guillette and Sullivan, 1985; Vitt and Cooper, 1985). However, fat bodies were almost exhausted in females that had finished the first vitellogenesis and remained vestigial throughout the reproductive season, so energy allocated to vitellogenesis in later clutches seems to be obtained directly from food consumed during that period.

In lizards, lipid storage is an important mechanism to compensate for seasonal fluctuations in food supply, allowing the use of reserves accumulated during periods of high prey availability when required for breeding or overwintering (Derickson, 1976a; Duvall et al., 1982; Nagy, 1983). Primary utilization of lipid stores for reproduction is assumed when mature females have distinctly larger fat bodies than males and there is a decrease of stores throughout the reproductive season (Hahn and Tinkle, 1965; Ballinger, 1973; Diller and Wallace, 1984). This seems to apply to lacertids from southwestern Europe, as these species show moderate reductions in fat body size during the winter but an abrupt decrease at the beginning of the reproductive season (Braña, 1983; Argüello, 1990; Braña et al., 1990; Castilla and Bauwens, 1990).

In the species studied here, vitellogenesis begins shortly after emergence from winter inactivity, at a time of low food availability and with daily activity greatly restricted by the unfavorable thermal environment. Stomach repletion level showed important differences throughout the reproductive period, suggesting low feeding activity at the beginning of the spring emergence. For specimens caught from March to April, the period during which first vitellogenesis occurs, the numbers of prey items per stomach were significantly lower than the corresponding values for the period from May to July, when successive clutches develop (Table 1; $t = 6.97$, $df = 38$ for *P. bocagei*; $t = 13.69$, $df = 43$ for *P. muralis*; and $t = 12.05$, $df = 50$ for *L. monticola*; $P < 0.001$ in all cases). The difference in stomach content indicates reduced trophic activity in the first period, especially considering that low environmental temperatures during this period could increase the transit time of food. Therefore, utilization of stored lipids for follicular enlargement in the first vitellogenesis signifies anticipation of the first ovulation, allowing females to lay more clutches per season (Ballinger, 1977; Derickson, 1976b), or even to reproduce in time for single-brooded populations. Furthermore, early (in the season) reproduction, associated with earlier hatching, results in increased growth of juveniles prior to hibernation. Growth prior to the first winter may enhance survivorship and future reproductive success (Bauwens and Verheyen, 1985), and reduce age at first reproduction (Heulin, 1985), also with potential advantages in lifetime reproductive success (Vinegar, 1975).

LITERATURE CITED

ARGÜELLO, J. A. 1990. Biología reproductiva de *Lacerta monticola* en una población de la Cordillera Cantábrica. Graellsia 46:253–261.

BALLINGER, R. E. 1973. Comparative demography of two viviparous iguanid lizards (*Sceloporus jarrovi* and *Sceloporus poinsetti*). Ecology 54:269–283.

———. 1977. Reproductive strategies: food availability as a source of proximal variation in a lizard. Ecology 58:628–635.

BAUWENS, D., AND R. F. VERHEYEN. 1985. The timing of reproduction in the lizard *Lacerta vivipara*: differences between individual females. J. Herpetol. 19:353–364.

Braña, F. 1983. La reproducción en los saurios de Asturias: ciclos gonadales, fecundidad y modalidades reproductoras. Rev. Biol. Univ. Oviedo 1:29–52.

———, M. J. Arrayago, A. Bea, and A. Barahona. 1990. Ciclo reproductor y de cuerpos grasos en los machos de *Lacerta monticola cantabrica.* Comparación entre dos poblaciones situadas a diferente altitud. Amphibia-Reptilia 11:41–52.

Cale, W. G., and J. W. Gibbons. 1972. Relationships between body size, size of the fat bodies, and total lipid contents in the canebrake rattlesnake (*Crotalus horridus*) and the black racer (*Coluber constrictor*). Herpetologica 28:51–53.

Castilla, A., and D. Bauwens. 1990. Reproductive and fat body cycles of the lizard, *Lacerta lepida* in central Spain. J. Herpetol. 24:261–266.

Congdon, J. D., and D. W. Tinkle. 1982. Reproductive energetics of the painted turtle (*Chrysemys picta*). Herpetologica 38:228–237.

Derickson, W. K. 1976a. Lipid storage and utilization in reptiles. Amer. Zool. 16:711–723.

———. 1976b. Ecological and physiological aspects of reproductive strategies in two lizards. Ecology 57:445–458.

Diller, L. V., and R. L. Wallace. 1984. Reproductive biology of the northern Pacific rattlesnake (*Crotalus viridis oreganus*) in northern Idaho. Herpetologica 40:182–193.

Duvall, D., L. J. Guillette, and R. E. Jones. 1982. Environmental control of reptilian reproductive cycles. *In* C. Gans and F. H. Pough (eds.), Biology of the Reptilia, Vol. 13, pp. 201–231. Academic Press, New York.

Etheridge, K., L. C. Wit, J. C. Sellers, and S. E. Trauth. 1986. Seasonal changes in reproductive condition and energy stores in *Cnemidophorus sexlineatus.* J. Herpetol. 20:544–559.

Guillette, L. J., and D. A. Bearce. 1986. The reproductive and fat body cycles of the lizard, *Sceloporus grammicus disparilis.* Trans. Kansas Acad. Sci. 89:31–39.

———, and G. Casas-Andreu. 1981. Seasonal variation in fat body weights of the Mexican high elevation lizard *Sceloporus grammicus microlepidotus.* J. Herpetol. 15:366–371.

———, and W. P. Sullivan. 1985. The reproductive and fat body cycles of the lizard, *Sceloporus formosus.* J. Herpetol. 19:474–480.

Hahn, W. E., and D. W. Tinkle. 1965. Fat body cycling and experimental evidence for its adaptive significance to ovarian follicle development in the lizard *Uta stansburiana.* J. Exp. Zool. 158:79–86.

Heulin, B. 1985. Maturité sexuelle et âge à la première reproduction dans une population de plaine de *Lacerta vivipara.* Can. J. Zool. 63:1773–1777.

Jameson, E. W., and A. Allison. 1976. Fat and breeding cycles in two montane populations of *Sceloporus occidentalis* (Reptilia, Lacertilia, Iguanidae). J. Herpetol. 10:211–220.

Nagy, K. A. 1983. Ecological energetics. *In* R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.), Lizard Ecology. Studies of a Model Organism, pp. 25–54. Harvard Univ. Press, Cambridge, Massachusetts.

Saint Girons, H., and R. Duguy. 1970. Le cycle sexuel de *Lacerta muralis* L. en plaine et en montagne. Bull. Mus. nat. Hist. Naturelle 42:609–625.

Salvador, A. 1985. Guía de Campo de los Anfibios y Reptiles de la Península Ibérica, Islas Baleares y Canarias. S. García, León, Spain. 212 pp.

Vinegar, M. B. 1975. Demography of the striped plateau lizard *Sceloporus virgatus.* Ecology 56:172–182.

Vitt, L. J., and W. E. Cooper. 1985. The relationship between reproduction and lipid cycling in the skink *Eumeces laticeps* with comments on brooding ecology. Herpetologica 41:419–432.

———, and S. R. Goldberg. 1983. Reproductive ecology of two tropical iguanid lizards; *Tropidurus torquatus* and *Platynotus semitaeniatus.* Copeia 1983: 131–141.

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Food Habits of Three Syntopic Reptiles from the Barahona Peninsula, Hispaniola

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Sauresia agasepsoides (Sauria: Anguidae), *Amphisbaena gonavensis* (Amphisbaena: Amphisbaenidae), and *Typhlops syntherus* (Serpentes: Typhlopidae) are found syntopically in the xeric lowlands of the Barahona Peninsula, Dominican Republic. Little is known of their natural histories. Schwartz and Henderson (1991) and Thomas (1965a, b, c) described habitat. Thomas (1965c) documented the syntopic association between *A. gonavensis* and *T. syntherus.* Food habits of *A. gonavensis* were described by Cusumano and Powell (1991). Thomas (1965b) described captive *A. gonavensis* as "voracious" feeders. Locomotor activity was documented in *Amphisbaena* (including *A. gonavensis*) and *Typhlops* by Thomas and Thomas (1978).

Vegetation on the Peninsula (sensu Henderson and Schwartz, 1984) consists mainly of species associated with subtropical dry and thorn forest (Hoppe, 1989). These generally xeric woods are characterized by deciduous trees of moderate to large size, thorny shrubs, largely represented by the genus *Acacia,* and an undergrowth of cacti and succulents, such as *Opuntia, Melocactus,* and *Agave. Typhlops syntherus* may extend into a more mesic habitat, characterized by *Acacia* and

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