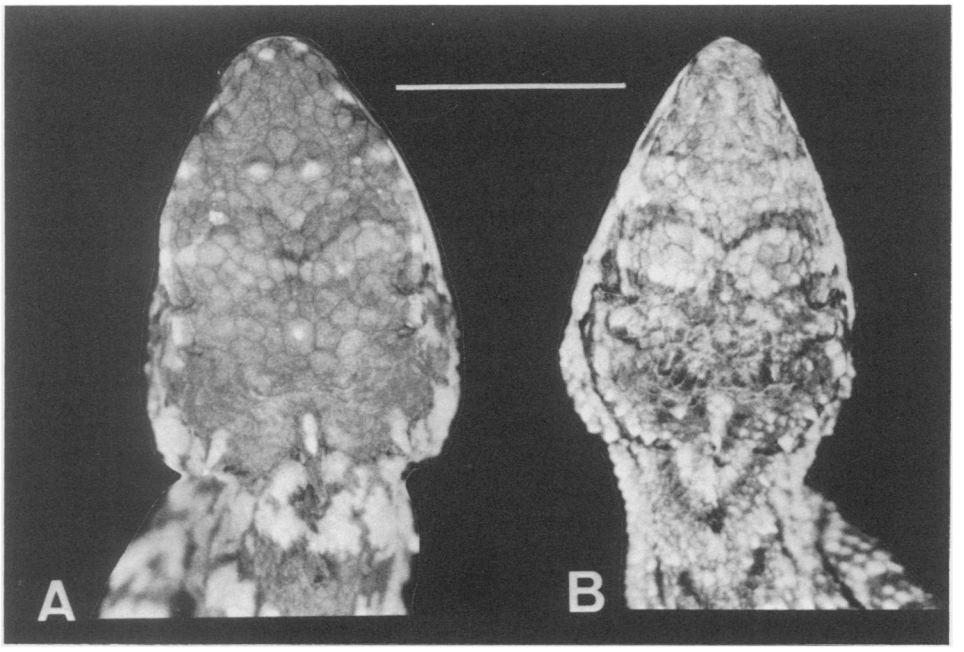

FIG. 3. Dorsal views of heads of *Japalura chapaensis* (holotype; A), and *J. swinhonis* (KUZ R2933; B). The scale indicates 10 mm.

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Physiological Color Change in Snakes

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Among reptiles, physiological color change is well known in lizards (Parker, 1948; Porter, 1972; Bagnara and Hadley, 1973), and has been reported in turtles (Woolley, 1957) and snakes. It usually involves the rapid (minutes to hours) movement of melanosomes into (darkening) or out of (lightening) dermal melanophore processes. Morphological color change is a longer process (days to weeks) and involves an absolute increase in melanosomes and melanophores (Bagnara and Hadley, 1973; Moll et al., 1981).

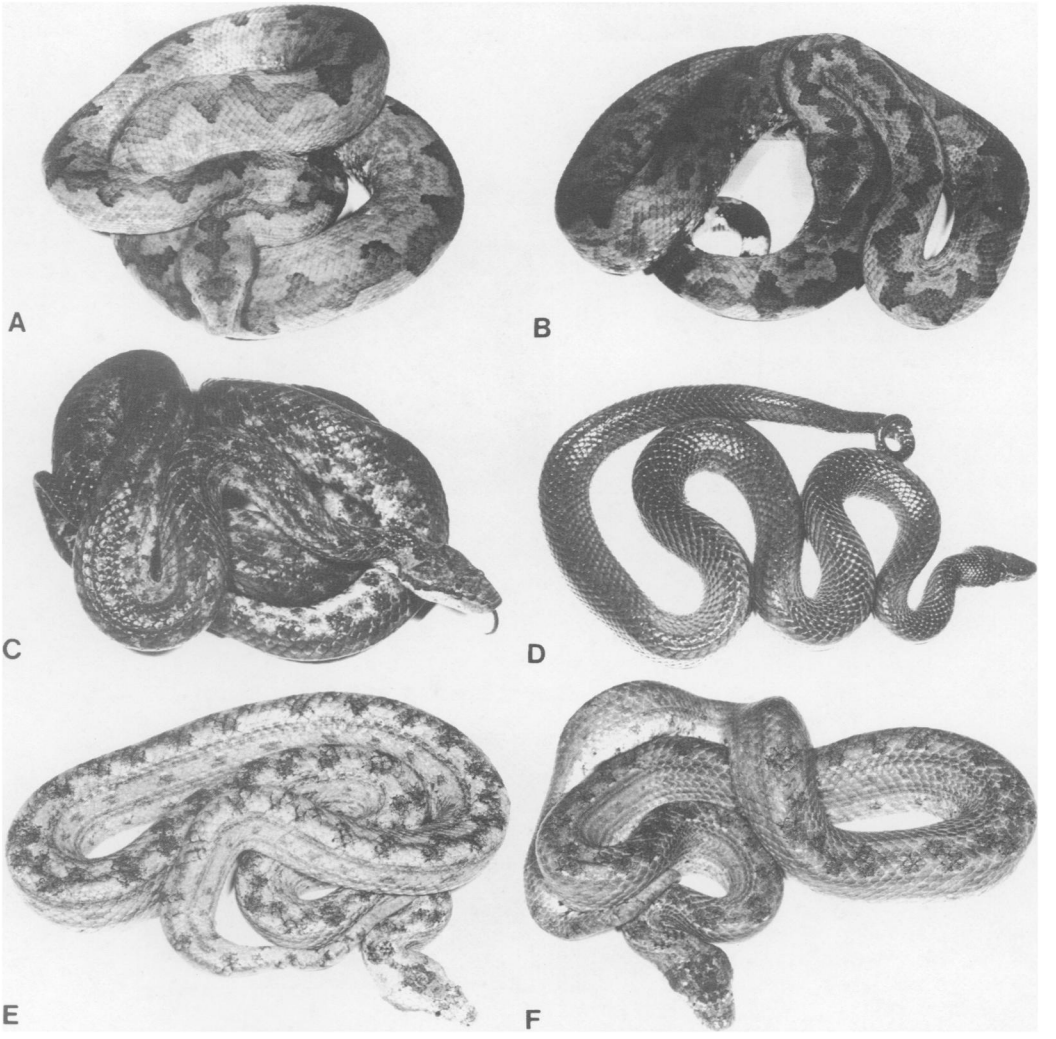

FIG. 1. Three individual snakes photographed in light phase (A, C, E) and dark phase (B, D, F): *Candoia carinata* (A, B), *Tropidophis haetianus* (C, D), and *T. melanurus* (E, F).

Color change in snakes appears to be very uncommon. Seasonal change has been observed in three Australian elapids (Banks, 1981; Mirtschin and Davis, 1982) and in the viperid *Vipera berus* (Rehák, 1987), and apparently involves morphological color change (Waring, 1963). In the thread snake *Leptotyphlops dulcis* (Leptotyphlopidae), rapid color change is a defensive behavior achieved by elevating the scales (Gehlbach et al., 1968). A similar type of color change in *L. scutifrons* (Visser, 1966) probably involves the same mechanism.

Rahn (1941) was able to induce physiological color change in snakes from the families Viperidae (1 species) and Colubridae (4 species). However, naturally-occurring physiological color change has been described in only three species of snakes: *Casarea dussumieri* (Bolyeriidae; McAlpine, 1983), *Tropidophis feicki* (Tropidophiidae; Rehák, 1987), and *Crotalus viridis* (Viperidae; Klauber, 1930, 1956; Sweet, 1985). Here, we describe the phenomenon in three additional species: *Candoia carinata* (Boidae), *Tropidophis haetianus*, and *T. melanurus*. Common aspects of these six species, and three other species for which physiological color change has been mentioned, are reviewed.

An adult female (508 mm snout-vent length [SVL]) *Candoia carinata* (locality unknown) was obtained in April 1986. After color change was noted, the snake was maintained under fluorescent light for approximately 11–13 hr per day and spot checks for coloration were made at about 1-hr intervals over a one week period (1–8 May 1986). In the light phase (Fig. 1A), the dorsal ground color was light tan with dark tan to grayish-brown middorsal blotches. Dorsolateral blotches or mottling were barely evident. In the dark phase (Fig. 1B), the dorsal ground color was dark tan to brown with dark brown to black, irregularly-shaped blotches forming a relatively continuous middorsal band. A majority of observations (13/17) made during

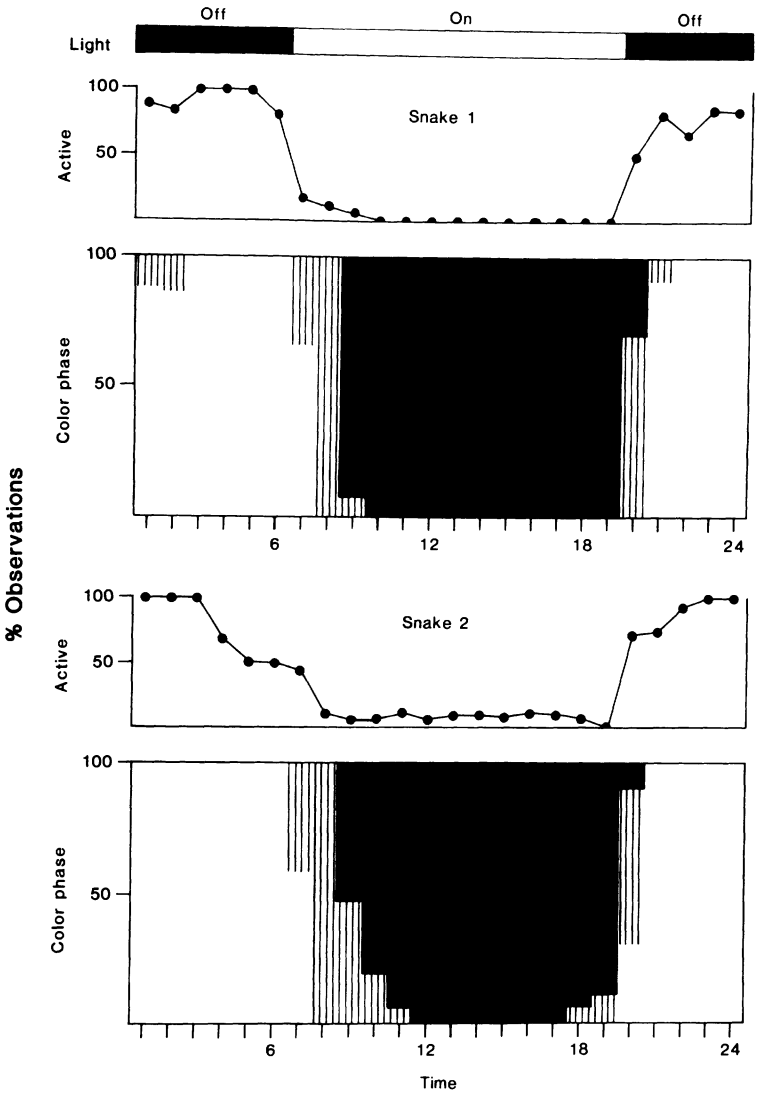

FIG. 2. Color change and activity patterns in two *Tropidophis melanurus* under a controlled light cycle (13L: 11D). Bar at top indicates light cycle. Values are averages of observations (N = 330, total) during 5 wk experiment. For color phase: white = light phase; black = dark phase; and vertical lines = transitional.

lighted hours revealed the snake in its dark phase, whereas a majority of the observations (5/7) made during dark hours revealed the snake in its light phase. The shortest period recorded for a complete transition from one phase to the other (in this case, dark to light) was 140 min.

We obtained an adult female (486 mm SVL) *Tropidophis haetianus* from a resident of Quick Step, Trelawny Parish, Jamaica on 9 October 1984. The snake was collected during the day and the collector believed it to be a young black snake (*Alsophis ater*). However, when we arrived at 2130 hr (after dark) and examined the snake, it had a yellow ground color with two rows of dark dorsal markings and we were suprised that it had been confused with *Alsophis*, a much darker snake. The following morning, the reason for the apparent confusion became obvious when the snake was again examined and found to be almost completely black. After return to the laboratory, it was maintained alive for 19 days during which only occasional observations were made. In the light phase (Fig. 1C), the dorsal ground color was yellow and heavily patterned with dark green, reddish-brown, brown, and black markings. In the dark phase (Fig. 1D), the dorsal surface was entirely black with virtually no trace of a pattern.

Two adult *Tropidophis melanurus* (snake 1 = 395 mm SVL; snake 2 = 420 mm SVL) were collected in March 1987 on Guantanamo Bay Naval Station, Cuba. Color change was noticed soon after capture. In the light phase (Fig. 1E), the dorsal ground color was a grayish pink, and the dorsal markings were a greenish brown. The dorsal pattern was composed of a series of blotches along a middorsal stripe. In the dark phase (Fig.

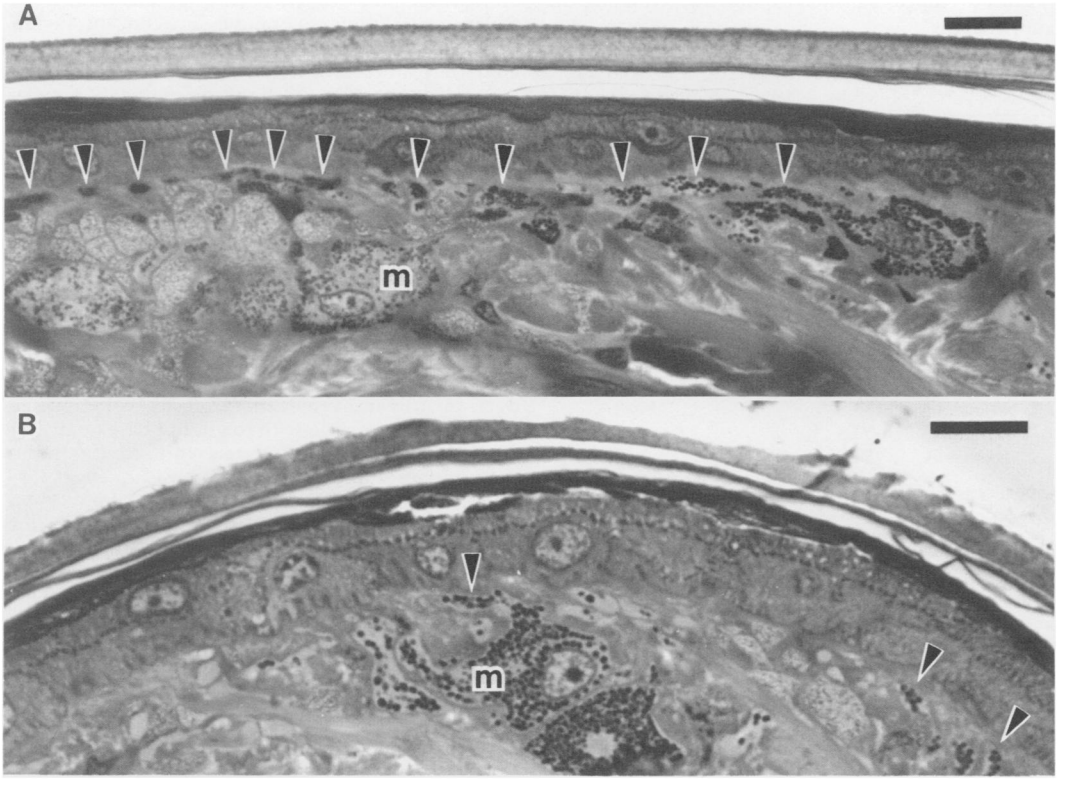

FIG. 3. Cross sections of two scales (removed 12 hr apart) from the dorsolateral region of a living *Tropidophis melanurus* (dark bars = 10 μm). A) Dark phase: melanosomes fill the melanophore processes (arrowheads) just below the epidermis, leaving fewer in the melanophore body (m). B) Light phase: melanosomes are concentrated in the melanophore body, with relatively few in the processes. Portions of other melanophores also are visible in both sections.

1F), the pattern was barely discernible as the ground color darkened to a light brown.

A light cycle experiment was performed with the two specimens of *Tropidophis melanurus*. They were placed on a 13L:11D light cycle within a week after capture, and housed in wide-mouth gallon jars with paper toweling. Observations (N = 330) on coloration and activity were made as often as possible during the course of the study (10 April–16 May 1987) and were taken on the hr (±10 min). A flashlight was used for observations made during the dark hours. Snake color was assigned to one of three categories: light, transition, and dark. Snakes were considered "active" when prowling, or (more commonly) resting with the head oriented above the body (ca. 45° angle) and protruding from the paper toweling. Snakes were scored as "inactive" if they were completely concealed in the paper toweling, or if exposed, they were motionless and their head was flat on the substrate.

Color change in *Tropidophis melanurus* closely followed a 24-hr light and activity cycle (Fig. 2). When the lights were off, the snakes usually were active and in the light phase. When the lights were on, the snakes generally were inactive and dark. Complete color change took between 90 min (dark to light phase) and 120 min (light to dark phase) after the lights went off (or on). The level of activity changed much more quickly, often within minutes after a change in the lights. The only times that the snakes were observed moving were during the first three hours in darkness. They usually rested during the dark hours with their head held up at an angle, probably typical of "sit-and-wait" predators. When the lights went on, the snakes would respond relatively quickly, withdrawing their heads into the paper toweling within a few minutes. The strongest evidence that color change was directly correlated with activity was obtained when the snakes were fed, or prior to shedding. Activity usually ceased after feeding and the snakes would remain dark and inactive for 24–48 hr. Color change data obtained after feeding and before shedding were not included in Fig. 2.

The primary mechanism for rapid color change in lizards involves the movement of melanosomes (pigment-containing organelles) within dermal melanophores (Bagnara and Hadley, 1973). A dermal chromatophore unit is composed of iridophores layered between a xanthophore above and a melanophore below. Finger-like projections (processes) of the melanophore extend up around the iridophores and lie external to the xanthophore. The actual color change (darkening) occurs when the melanosomes migrate

TABLE 1. Species of snakes showing physiological color change.

	24-hr cycle	Habits[1]	Distribution[2]	Reference[3]
Boidae				
Candoia carinata	YES	T	I	1
Bolyeriidae				
Casarea dussumieri	YES	T	I	2
Tropidophiidae				
Tropidophis canus	YES	T?	I	3
T. feicki	YES	A	I	3
T. greenwayi	YES	T	I	3
T. haetianus	YES	T	I	1, 3
T. melanurus	YES	T	I	1, 3, 4
Viperidae				
Crotalus cerastes	?	T	M	5
C. viridis	?	T	M	5, 6, ,7

[1] T = terrestrial, A = arboreal; data from Lynn and Grant (1940), Klauber (1956), Pope (1961), Minton and Minton (1973), Schwartz (1975), McCoy (1980), McAlpine (1983), Rehák (1987), and personal observations.

[2] M = mainland, I = insular.

[3] (1) this study; (2) McAlpine, 1983; (3) Rehák, 1987; (4) Lando and Williams, 1969; (5) Klauber, 1930; (6) Klauber, 1956; and (7) Sweet, 1985.

up these melanophore processes and are brought closer to the epidermis while partially blocking the xanthophore and iridophores (Bagnara and Hadley, 1973, figs. 2-23). This can be under hormonal control (*Anolis*) or both hormonal and neural regulation (*Chamaeleo* and *Phrynosoma*). Hormonal control of melanosome dispersion in dermal melanophores has been suggested for snakes (Rahn, 1941).

In order to determine whether color change in snakes followed the dermal chromatophore unit model, we sectioned scales of *Tropidophis melanurus*. Two scales were removed from the dorsolateral region of snake No. 2: one scale during the light phase and the other during the dark phase (12 hr later). After removal, the scales were quickly transferred to light-retardant specimen vials containing 2% glutaraldehyde in 0.1 M cacodylate buffer, pH 7.4, at room temperature. Subsequent steps followed standard electron microscopy protocol and included a postfix with 1% osmium tetroxide in 0.1 M cacodylate buffer, dehydration through a graded series of ethanol solutions, and embedding in Epon 812. Multiple sections, 0.75 μm thick, were cut on a Reichert Ultracut ultramicrotome with glass knives, and placed on microscope slides. The sections were then either viewed directly with phase contrast optics or were stained with a polychrome stain and observed with brightfield optics on a Zeiss Photomicroscope I.

Examination of multiple sections from the two scales of *Tropidophis melanurus* (snake No. 2) revealed differences in dermal melanophore structure corresponding to predictions based on the dermal chromatophore unit. In the dark phase (Fig. 3A), melanosomes (pigment granules) are concentrated in the melanophore processes which line the base of the epidermis, and relatively few are seen in the body of the melanophore. In the light phase (Fig. 3B), melanosomes appear concentrated in the body of the melanophore and not in the processes. Sections taken from different portions of each scale were consistent in these features.

Physiological color change has been recorded in nine species of snakes in four families (Table 1). In addition to those published records, it has been observed in *Boa constrictor* (B. Bechtel, pers. comm.; J. Murphy, pers. comm.), *Candoia bibroni* (J. Murphy, pers. comm.), and several species of colubrids (S. Sweet, pers. comm.). Although it probably will be recorded in additional species, several patterns are now evident. In at least seven of those species, color change followed a 24-hr cycle with the light phase occurring during the night and associated with activity. In the three species studied in detail (*Casarea dussumieri, Tropidophis feicki,* and *T. melanurus*), snakes were inactive and remained in the dark phase for several days prior to shedding, and in at least one species (*T. melanurus*), color change was associated with feeding. These observations suggest a direct correlation between color change and activity. However, in *Crotalus viridis*, resting snakes lightened rapidly (2-4 min) with increased temperature or activity, regardless of time of day (Sweet, 1985; pers. comm.).

Seven of the species showing physiological color change are restricted to islands: the West Indies (*Tropidophis* spp.); Round Island, Indian Ocean (*Casarea*); and the islands of the southwest Pacific (*Candoia*). Also, most are relatively small in body size (30-80 cm SVL) and terrestrial in habits. Thus physiological color change in snakes appears to be associated with small, terrestrial, island "boas," and cyclic (24 hr) color change is known only in those species. However, the presence of physiological color change in four diverse snake families suggests that it is a widespread phenomenon that will require further documentation and experimentation before it is completely understood.

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Should Hindgut Contents Be Included in Lizard Dietary Compilations?

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Several studies of prey consumption in lizards have used hindgut contents in addition to stomach contents to estimate diet (e.g., Schoener, 1967, 1968; Schoener and Gorman, 1968). This procedure can greatly increase sample size. Additionally, this procedure may reduce bias in estimating prey-size distributions in the following way. Individual large prey may pass through the stomach at a rate less than that of individual small prey, so that at any moment pieces of an individual large prey item are more likely to be found in both the stomach and hindgut. Hence, counting only prey in the stomach may bias the prey-size distribution towards large prey (Schoener, 1967; a bias may exist for the entire tract as well, but it will be smaller). The procedure of including hindgut contents in lizard dietary compilations has been criticized by Floyd and Jenssen (1984) as having its own bias, specifically that soft-bodied prey are more likely to have disintegrated beyond detection by the time they reach the hindgut than are hard-bodied prey. Using their own study of *Anolis opalinus* (Floyd and Jenssen, 1983), they argued that this bias has three effects: 1) the taxonomic diversity of prey (measured as $\bar{H} = -p_i \log[p_i]$, where p_i is the decimal frequency of the ith prey category) is substantially less in the hindgut than in the stomach; 2) the size diversity of prey is likewise; and 3) hindgut contents are biased toward smaller prey, because soft-bodied prey tend to be large, not because of the argument given in Schoener (1967).

Because the criticisms of Floyd and Jenssen are specifically directed toward my studies, and because biases of the order they found for their study are serious, I re-analyzed some of my data (whose summary characteristics have already been published) to determine the magnitude, if any, of their three effects. Because it is important to have some statistical assessment of differences between stomach and hindgut contents, data were analyzed separately for each of a number of lizard groups. The largest study meeting this requirement was for two Grenadan species, *Anolis richardi* and *Anolis aeneus* (Schoener and Gorman, 1968). It seemed most appropriate to distinguish here those lizard groups distinguished in the previous paper (Schoener and Gorman, 1968), as they were the entities about which conclusions were drawn. Three groups—adult males, adult females and subadult males (males spanning roughly the same size as adult females)—were so distinguished for each species. These six groups have large sample sizes, from 287 to 4592 items each; they have the additional advantage that they span a large range of lizard sizes, larger than the single comparison made by Floyd and Jenssen (which lumped all classes of *A. opalinus*).

In my original prey records, stomach contents were distinguished from hindgut contents, so that the two can be separated here for an analysis mimicking that