vor individuals that delay maturity; in a growing population, it may favor immediate maturity (*19*). Growing populations are characterized by a high ratio of juveniles to adults while declining populations contain many adults and few juveniles (*1*). Presumably, a juvenile determines the growth rate of the population by its social interactions with adults and juveniles. If most interactions are with smaller, therefore younger, juveniles, this indicates that the population is growing and maturation is initiated as soon as possible. If, however, most interactions are with adults or larger, therefore older, juveniles, this indicates that the population is declining and maturity is delayed.

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References and Notes

1. L. Cole, *Q. Rev. Biol.* **29**, 103 (1954); R. C. Lewontin, in *The Genetics of Colonizing Species*, H. G. Baker and G. L. Stebbins, Eds. (Academic Press, New York, 1959), pp. 77–94.
2. G. Alm, *Inst. Freshwater Res. Drottingholm* **40**, 5 (1959); M. Gadgil and W. H. Bossert, *Am. Nat.* **104**, 1 (1970); R. Green and P. R. Painter, *ibid.* **109**, 1 (1975).
3. K. D. Kallman and M. P. Schreibman, *Gen. Comp. Endocrinol.* **21**, 287 (1973).
4. D. Grobstein, *Univ. Calif. Publ. Zool.* **47**, 1 (1940).
5. R. L. Borowsky, *Nature (London)* **245**, 332 (1973).
6. J. Sohn, *Copeia*, in press.
7. If dominant fish matured earlier than fish reared in isolation, there would be acceleration of maturity.
8. There are three types of females (WY, WX, and XX) and two types of males (XY and YY). XY males mated with WX females produce a 1:3 sex ratio, while XX females mated with YY males produce only males [K. D. Kallman, *Zoologica* **50**, 151 (1965)].
9. The YY males were Belize stock (3492) and the XX females were Rio Jamapa stock ($163B^{47}$) obtained through the courtesy of K. D. Kallman, Osborn Laboratories of Marine Sciences, New York Aquarium.
10. Newly born fish were fed on a diet of nauplii, mosquito larvae, and frozen brine shrimp in excess.
11. The experimental period lasted from 13 November 1975 to 1 June 1976.
12. The stages of anal fin metamorphosis are as described by Kallman and Schreibman (*3*) and Grobstein (*4*).
13. The arrangements of tanks in the laboratory permitted direct observations from a distance of about 1 m. Observations were made before and after feeding. Each individual could be identified by its markings resulting from the phenotypic expression of the *Sp* (spotted side) pigment gene.
14. R. Baeninger, *Psychonom. Sci. Sect. Anim. Physiol. Psychol.* **10**, 185 (1968); J. C. Braddock, *Physiol. Zool.* **18**, 176 (1945).
15. The ages at maturity of four P^eP^e fish raised in isolation were 73, 86, 86, and 85 days. The ages at maturity of five P^eP^l fish raised in isolation were 116, 125, 124, 118, and 125 days.
16. The medians of the relative growth rates for the first and second fish to mature in experiments 1 and 2 were 0.018 and 0.019, respectively. They are not significantly different (Wilcoxon sign rank test, $t = 86$; $N = 19$).
17. D. F. Frey and R. J. Miller, *Behaviour* **42**, 8 (1972).
18. F. E. McKay, *Ecology* **52**, 778 (1971); J. Sohn, in preparation.
19. L. Demetrius, *Math. Biosci.* **4**, 129 (1969); D. B. Mertz, *Am. Nat.* **105**, 437 (1971).
20. I thank R. C. Lewontin and E. O. Wilson for helpful discussions.

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Natural Selection for Juvenile Lizards Mimicking Noxious Beetles

Abstract. *Adult* Eremias lugubris *in southern Africa are concealingly colored and move with a typical lizard gait, but the jet-black and white juveniles are conspicuous and forage actively with arched backs. In color, gait, and size, juveniles mimic "oogpister" beetles (Carabidae:* Anthia*) that spray an acidic, pungent fluid when molested. This unique mimicry, which is believed to be the first reported case of a terrestrial vertebrate mimicking an invertebrate, seems to reduce predation on juvenile lizards.*

Batesian mimicry, the important evolutionary phenomenon (*1, 2*) in which selection by predators favors individuals of a palatable or unprotected species (mimic) that deceptively resemble those of an unpalatable or protected species (model), is traditionally established by satisfying several correlative criteria (*3*) or by manipulative experiments in the field or laboratory (*4*). Despite widespread interest in the phenomenon, however, natural field evidence of the selective advantage of Batesian mimicry is scant (*5*). Here we present correlative evidence for a bizarre and apparently unique case of mimetic resemblance, that of a palatable juvenile lizard mimicking a noxious beetle (*6, 7*), as well as indirect field evidence that this mimicry reduces predation rates.

Adult *Eremias lugubris* in the Kalahari semidesert of southern Africa are pale red-tan, a color that blends with the Kalahari sand (Fig. 1C). In contrast, juvenile *E. lugubris*, jet-black above and below with broken whitish lateral and dorsal stripes (tails black basiventrally, thereafter buff to red-yellow), are quite conspicuous (Fig. 1A). Metamorphosis into the adult coloration begins at snout-to-vent lengths (SVL's) of about 40 mm and is generally complete at SVL's of 45 to 50 mm. Ontogenetic color shifts are common in *Eremias*, but one of this magnitude is unparalleled (*8*).

Adults and juveniles also differ in foraging gait. Adults forage actively (*9*) with lateral undulations typical of lacertid lizards. Juveniles also forage actively, but walk stiffly and jerkily with strongly arched backs and tails pressed to the substrate. (Bilateral contraction of muscles in the ventral midline apparently produces the arch.) Pronounced bending curves in the body and tail, associated with lateral undulations in the adults (and most lizards), are not apparent in juveniles. The largest juvenile observed walking this way was 49 mm SVL, near the upper size of color metamorphosis. The juvenile gait, which persists in captivity, seems to be unique among lizards.

The evolutionary significance of the conspicuous coloration and arch-walking gait of these juvenile lizards needs evaluation. Metamorphoses in coloration and gait are unrelated to reproductive maturity, as lizards mature several months later. Black coloration can confer thermoregulatory advantages to insects with insulated elytra (*10*) but is more likely to be a thermoregulatory disadvantage to a small lizard active only during hot summer and autumn months. Furthermore, because juveniles arch-walk at both high and low body temperatures (*11*), arch-walking cannot be a heat avoidance posture.

We propose that these juvenile lizards are in fact behaviorally and morphologically mimicking abundant, sympatric, noxious "oogpister" (*12*) beetles [Carabidae: *Anthia* spp. (*13*)], which squirt an acidic pungent fluid [5*N* formic acid plus isovaleraldehyde, acetic acid, tiglic acid, and so forth (*14*)]. Juveniles resemble oogpisters in aposematic (*15*) coloration [beetles (Fig. 1B) are black with lateral white stripes on the elytral borders, sometimes also on the thorax and head] (*16*), in size (beetles range from about 30 to 52 mm in length) (*17*), and in gait (oogpisters are active foragers) (*18*). Juvenile lizards metamorphose into the adult coloration and gait at sizes corresponding roughly to the maximum sizes of beetles.

Beetles are generally considerably more abundant than juvenile lizards, are active over broader time periods daily and perhaps seasonally (*19*), and may have a broader geographic range. These noxious beetles are thus ideal models (*3*); juvenile lizards have apparently converged on them both in behavior and morphology. Indeed, on occasion we have initially mistaken juvenile lizards for oogpisters!

The arch-walk may have evolved from an arched-back, facing-off posture sometimes used by adult *E. lugubris* in aggressive encounters. Many African *Eremias* juveniles are darker than adults (*8*), and the black coloration of *E. lugubris* juveniles probably evolved as an exaggeration of this trend. Numerous lizard predators could be selective agents, including birds (several shrikes, secretary birds), mammals (bat-eared foxes, jackals, suricates), and snakes (horned adders, sand snakes).

If juvenile lizards mimic oogpisters,

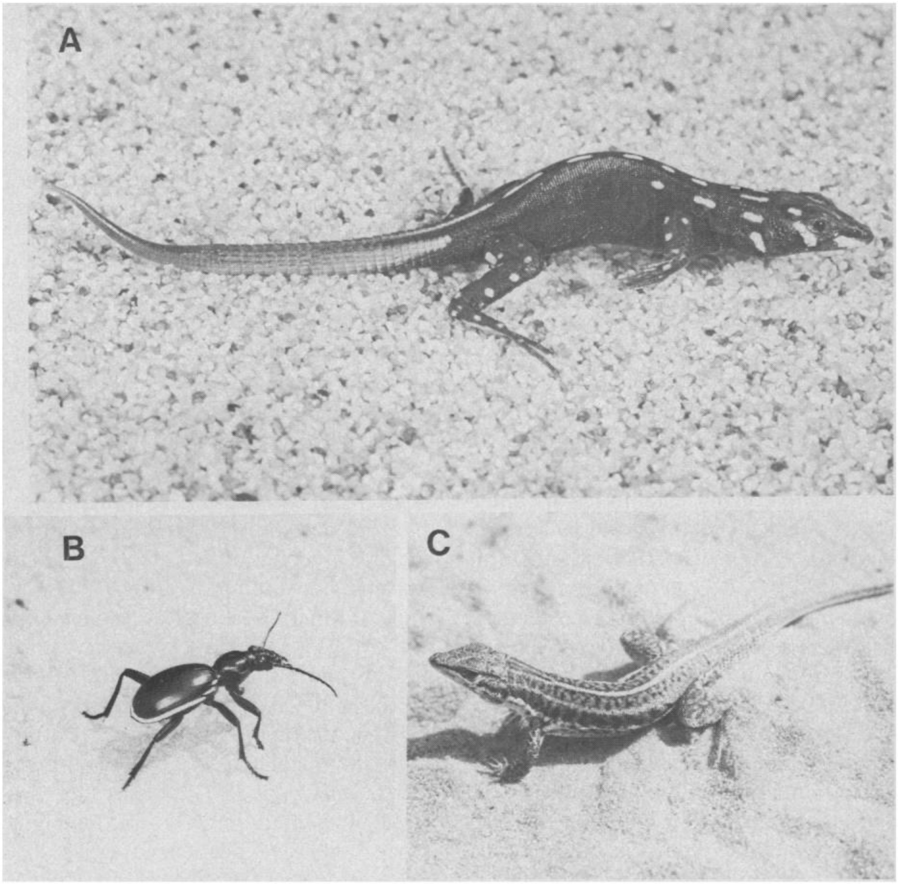

Fig. 1. (A) Lateral view of arch-walking juvenile *E. lugubris* (SVL about 35 mm) on beach sand. A normal tail would be concealingly colored on red Kalahari sand (the tip of this individual's tail is regenerated tissue). (B) View of oogpister beetle, *Anthia* (total length, 37 mm). (C) Adult *E. lugubris* (SVL about 60 mm). In both (B) and (C), the animals were photographed on Kalahari sand. [Fig. 1A from photograph by J. Hensel]

predation rates on these lizards should be lower than on sympatric nonmimetic *Eremias*. We cannot measure predation rates directly, but the frequency of broken tails can be used to index relative intensity of predation (*20*). Despite foraging actively, juvenile *E. lugubris* have the lowest frequency of broken tails of all sympatric juvenile *Eremias* in the southern Kalahari (*21*).

The only quadrupedal lizards previously suspected of being mimics are two terrestrial geckos that sometimes arch their tails over their backs when disturbed and may mimic scorpions (*22*). Alternatively, this posture may merely divert predators from more vital body parts (*23*).

Our data (juvenile *E. lugubris* differ markedly from close relatives in coloration and behavior; juveniles resemble oogpister beetles in color, size, and gait; daily activity periods and probably both seasonal activity period and geographic range of juvenile lizards are entirely contained within those of the beetles; juveniles are less abundant than beetles; and juveniles have a relatively low frequency of broken tails) satisfy traditional criteria (*3*, *24*) that strongly suggest Batesian mimicry. The resemblance of juvenile *E. lugubris* to oogpister beetles represents not only the first substantive case of mimicry involving a quadrupedal lizard, but also, to the best of our knowledge, the first case of a terrestrial vertebrate mimicking an invertebrate [(*6*, *7*), but see also (*22*, *23*)]. More importantly, our indirect evidence that mimicry is associated with reduced predation provides one of the few nonmanipulative examples supporting the hypothesis that natural selection promotes Batesian mimicry (*5*).

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References and Notes

1. R. A. Fisher, *The Genetical Theory of Natural Selection* (Dover, New York, 1958), p. 163.
2. P. M. Sheppard, *Cold Spring Harbor Symp. Quant. Biol.* **24**, 131 (1959); E. B. Ford, *Ecological Genetics* (Chapman and Hall, London, 1964), p. 201.
3. Mimetic resemblance is not due to systematic affinity, mimics differ from close relatives, mimics and models are sympatric, models are more abundant than mimics, models and mimics are conspicuous, and only models are noxious or protected (*1*, p. 173). All are not, however, necessary conditions [J. V. Z. Brower, *Am. Nat.* **94**, 271 (1960); C. S. Holling, *Mem. Entomol. Soc. Can.* **45**, 1 (1965); L. E. Bobisud and C. J. Potratz, *Am. Nat.* **110**, 121 (1967)].
4. L. P. Brower, J. V. Z. Brower, F. G. Stiles, H. J. Croze, A. S. Hower, *Science* **144**, 183 (1964); O. J. Sexton, *Behaviour* **15**, 244 (1960); T. C. Boyden, *Evolution* **30**, 73 (1976).
5. M. Edmunds, *Defense in Animals: A Survey of Anti-predator Defenses* (Longman, New York, 1974), p. 128.
6. Models for other vertebrate Batesian mimics are also vertebrates [H. R. Bustard, *Brit. J. Herp.* **4**, 22 (1968); C. Gans, *Evolution* **18**, 705 (1965); (*7*)]. Some invertebrates, however, mimic vertebrates or even vertebrate droppings [R. Morrell, *Malay Nat. J.* **9**, 94 (1954); M. Rothschild, in *Ecological Genetics and Evolution*, R. Creed, Ed. (Appleton-Century-Crofts, New York, 1971), p. 214].
7. J. E. Huheey and R. A. Brandon, *Herpetologica* **30**, 149 (1974).
8. G. A. Boulenger, *Monograph of the Lacertidae* (British Museum of Natural History, London, 1929), vol. 2, p. 239.
9. E. R. Pianka, R. B. Huey, L. R. Lawlor, in *Analysis of Ecological Systems*, D. J. Horn, R. Mitchell, G. R. Stairs, Eds. (Ohio State Univ. Press, Columbus, in press).
10. K. Henwood, *Science* **189**, 993 (1975).
11. Body temperatures of arch-walking juveniles range from 34.2° to 40.8°C and are very similar to those of adults in the same season (34.5° to 41.4°C).
12. "Oogpister," the vernacular name of these beetles in the southern Kalahari, translates euphemistically as "eye squirter."
13. Sympatric species of *Anthia* include *A. cinctipennis*, *A. aemiliana*, and *A. limbata* (P. Basilewsky, personal communication).
14. P. D. Scott, H. R. Hepburn, R. M. Crewe, *Insect Biochem.* **5**, 805 (1975).
15. G. A. K. Marshall and E. B. Poulton, *Trans. Ent. Soc. London* **1902**, 508 (1902); H. B. Cott, *Adaptive Coloration in Animals* (Methuen, London, 1940), p. 194.
16. Diagonal stripes on the head and neck and the concealingly colored tails of juvenile *E. lugubris* may create the impression of a segmented insectlike body. Patterns of dorsal white stripes on lizards and beetles are not, however, identical (Fig. 1, A and B).
17. See Huheey and Brandon (*7*) for a discussion of size correlations between mimics and models.
18. Details of this beetle-like locomotion are being analyzed cinematographically (J. Peterson and R. B. Huey, in preparation).
19. Beetles are active during all daylight hours, whereas juvenile lizards are normally active only in midmorning (0857 to 1243). Seasonal activity of *Anthia* in the southern Kalahari is undocumented, but our recollection is that beetles were active much longer than juvenile *E. lugubris* (the lizards were active only from January through May).
20. J. B. S. Haldane and J. Huxley, *Animal Biology* (Oxford Univ. Press, London, 1927), pp. 175–176; A. S. Rand, *Copeia* **1954**, 260 (1954); E. R. Pianka, *Ecology* **48**, 348 (1967); T. Papenfuss, in preparation; but see D. W. Tinkle and R. E. Ballinger, *Ecology* **53**, 580 (1973).
21. Tail-break frequencies of juvenile *Eremias* (< 50 mm SVL) in the southern Kalahari [*E. lugubris* 10.5 percent, $N = 86$; *E. lineo-ocellata* 22.3 percent, $N = 413$; *E. namaquensis* 34.8 percent, $N = 46$] show significant overall heterogeneity (*G* test, $P < .001$); and the value for *E. lugubris* differs significantly (*STP* test, $P < .05$) from those of other species. Both tests are described by R. R. Sokal and F. J. Rohlf [*Biometry* (Freeman, San Francisco, 1969), p. 599]. Both *E. lugubris* and *E. namaquensis* are widely foraging lacertids (*9*), but only the latter has a high frequency of broken tails.
22. V. FitzSimons and C. K. Brain, *Koedoe* **1**, 99 (1958); W. S. Parker and E. R. Pianka, *Copeia* **1974**, 528 (1974).
23. J. D. Congdon, L. J. Vitt, W. W. King, *Science* **184**, 1379 (1974).
24. Juvenile *E. lugubris* were palatable to a tame secretary bird that refused to attack *Anthia* beetles: thus juvenile lizards are not Müllerian mimics (that is, mutual convergence of protected or unpalatable prey). For a recent classification of mimetic resemblances see R. I. Vane-Wright [*Biol. J. Linn. Soc.* **8**, 25 (1976)].
25. We thank D. Dobkin, J. Peterson, S. Stearns, and D. B. Wake for comments on the manuscript; P. Basilewsky for information on identifications and distributions of beetles; S. J. Arnold

for discussion; C. K. Brain, W. D. Haacke, G. and M. Mills, and C. and E. LeRiche for assistance in Africa; and directors of Wildlife and National Parks (Botswana), National Parks Board (Republic of South Africa), and Nature Conservation (Cape Province) for permission to work in their respective areas. Research supported by the National Geographic Society, National Science Foundation (grant GB-8727), Los Angeles County Museum of Natural History, Miller Institute for Basic Research in Science, and the Museum of Vertebrate Zoology and Department of Zoology (University of California, Berkeley).

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Chloride Transport Across Isolated Opercular Epithelium of Killifish: A Membrane Rich in Chloride Cells

Abstract. *The opercular epithelium of* Fundulus heteroclitus *contains typical gill chloride-secreting cells at the high density of 4 × 10⁵ cells per square centimeter. When isolated, mounted as a membrane, and short-circuited, it actively transports chloride ions from the blood side to the seawater side of the preparation. This preparation offers a useful approach to the study of osmoregulation in bony fishes.*

Extrarenal salt secretion is the key to the seawater teleost's ability to maintain an internal salt concentration hypoosmotic to its environment. To date, this osmoregulatory mechanism has been studied either in intact animals or in isolated, perfused gills (*1*). However, neither of these preparations meets all the criteria necessary for the application of the short-circuit current technique classically used in the study of ion transport across epithelia. The gill and the opercular epithelium have similar electrical and cytological characteristics, but the short-circuited opercular epithelium of the killifish (*Fundulus heteroclitus*) offers a better biophysical approach to the study of osmoregulation in teleosts. This tissue is a stratified epithelium that includes a small fraction of pavement, mucous, and nondifferentiated cells, and 50 to 70 percent chloride-secreting cells (*2*–*4*). The chloride-secreting cells extend from the basal lamina to the external aquatic environment and interrupt the stratification. Each cell has a prominent apical crypt, a rich population of mitochondria, and an extensive, branching tubular system continuous with the basal and lateral plasma membrane; these cells are identical in fine structure to the chloride-secreting cells of the gill (*3*).

The epithelium lining the pharyngeal cavity of the seawater-adapted killifish (*5*) was dissected free of the bony operculum and mounted as a flat sheet in a Lucite chamber with an aperture of 0.07 cm^2 (*6*). When bathed in the appropriate salt solution (*7*), the transepithelial potential difference initially increased within an hour to between 10 and 40 mv (mean ± standard error = 24.0 ± 1.6; $N = 32$; seawater side negative) and remained relatively constant for several hours. These potential difference values are in good agreement with those measurements made in vivo between the seawater environment and the plasma in several species of teleosts (*1*), and are somewhat higher than those observed in isolated, perfused flounder gills bathed on both sides with Ringer solution (*8*). The short-circuit current (I_{sc}) increased in a manner similar to the potential difference and reached steady state levels between 70 and 340 μa/cm^2 (mean = 190.1 ± 13.1; $N = 32$) where it remained constant for several hours. The transepithelial d-c resistance, taken as the ratio PD/I_{sc} (where PD is the potential difference), ranged from 70 to 330 ohm-cm^2 (mean = 138.5 ± 9.2, $N = 32$) and had the tendency to increase slightly over the course of several hours. Initial current-voltage relationship studies across this tissue showed a linear response indicating that this tissue behaved as an ohmic resistor and justified the use of this ratio as an indicator of the total transepithelial d-c resistance. The procedure for short-circuiting and the isotope flux measurements used here are described elsewhere (*9*).

As shown in Fig. 1a and Table 1, nitrogen-induced anoxia caused a significant ($P < .01$) reduction in the I_{sc} and potential difference, which was quickly reversed with the reintroduction of oxygen into the system. The substitution of chloride ion with the nonpenetrating methylsulfate anion in the solutions bathing both sides of the epithelium (Fig. 1b and Table 1) caused a rapid and significant ($P < .005$) decline in both the I_{sc} and potential difference to near zero values which were readily reversed with the reintroduction of chloride ions into the

Table 1. Chloride ion substitution and the effect of chloride transport inhibitors on the isolated opercular epithelium of *F. heteroclitus*. The data are expressed as means ± standard error. Numbers of experiments are in parentheses; R, resistance.

Experiment	Average I_{sc} (μa/cm^2)	Average PD (mv)	Average R (ohm-cm^2)	Average time to maximum effect (minutes)
Control (6)	234.4 ± 30.5	26.1 ± 4.0	122.7 ± 20.5	
Chloride free	8.8 ± 3.9	1.9 ± 0.6	58.5 ± 40.0	27
Percentage change	96.3	92.7	52.3	
Chloride rich	224.5 ± 27.8	23.5 ± 2.5	121.3 ± 28.9	5
Control (4)	236.6 ± 4.7	26.3 ± 2.5	110.7 ± 9.8	
Anoxia, N_2	39.6 ± 10.4	8.6 ± 1.7	269.2 ± 74.7	30
Percentage change	83.3	67.3	143.2	
Oxygenation	233.0 ± 14.7	30.8 ± 2.6	131.9 ± 5.3	11
Control (4)	186.4 ± 39.1	30.9 ± 4.0	186.3 ± 46.2	
Furosemide, $10^{-3}M$	22.9 ± 13.1	3.6 ± 1.2	173.3 ± 69.1	30
Percentage change	84.3	88.3	7.0	
Control (4)	139.7 ± 40.9	18.2 ± 4.1	141.6 ± 24.2	
Ouabain, $10^{-5}M$	15.9 ± 9.9	1.3 ± 0.8	79.4 ± 10.6	87
Percentage change	88.6	92.9	43.9	
Control (2)	115.4 ± 8.3	17.7 ± 6.5	150.2 ± 45.6	
Thiocyanate, $10^{-2}M$	60.0 ± 6.4	10.5 ± 3.9	169.1 ± 47.8	24
Percentage change	48.0	40.7	12.6	

Table 2. Fluxes of Cl^- across the isolated, short-circuited opercular epithelium of *F. heteroclitus*. The data are expressed as means ± standard error. Numbers of experiments are in parentheses. The average unidirectional $^{36}Cl^-$ fluxes across the paired preparations were significantly different from each other ($P < .01$) while the difference between the average I_{sc} for the paired preparations was not significant ($P > .90$).

Fluxes [μeq (cm^2)$^{-1}$ hour^{-1}]			Net flux (μa/cm^2)	Average I_{sc} (μa/cm^2)	[HCO_3^-] (mM)
Outflux	Influx	Net flux			
8.325 ± 1.668 (6)	1.162 ± 0.132 (6)	7.163 ± 1.739	191.9 ± 46.6	183.8 ± 21.8	16
3.452 ± 0.131 (2)	1.929 ± 0.009 (2)	1.523 ± 0.140	40.8 ± 3.7	39.0 ± 4.8	4