INFLUENCE OF INCUBATION CALLS ON POST-HATCHING RESPONSES OF PHEASANT CHICKS

E. D. BAILEY

ABSTRACT.—Ring-necked Pheasant (*Phasianus colchicus*) chicks exposed to a hen incubation vocalization during the final week of incubation showed stronger attraction to feeding and caution calls than expected by chance when tested one, three and five days post-hatching. Control chicks incubated in silence did not differ from chance in response to the caution call. Largest differences between experimental and control chicks for positive responses to the caution call occurred at one and three days post-hatching. Differences for positive response to the feeding call were greatest at one and five days post-hatching.

Correct pecking behavior in response to feeding calls was greater at all test ages in chicks exposed to incubation calls than in control chicks. However, when tested on the caution call, control chicks responded with correct hiding behavior more often than experimentals at one day of age. Correct behavior in response to the caution call greatly increased in experimental chicks at three days post-hatching but not in controls. By five days post-hatching, experimentals and controls were nearly equal. Calls by the incubating hen pheasant act to sensitize and predispose embryonic chicks for proper responses to calls that they will hear after hatching. Stages of post-hatching development and learning possibly have some modifying influence on the timing of responsiveness to post-hatching calls.

Kuo (1921, 1932) was the first to suggest that at least some features of apparently innate behavior of neonatal animals might be the result of experiences that occurred during late embryonic stages. Exposure of developing embryos to various sounds including self-auditory stimulation, sound stimulation by siblings and extra-egg sound sources has been shown to affect recognition of parent calls after hatching (Gottlieb 1965, 1971, 1974, 1975a, b, c, 1978) in domestic chickens (*Gallus gallus* var. *domesticus*), domestic Pekin ducks (*Anas platyrhynchos* var. *domesticus*) and Wood Ducks (*Aix sponsa*). Mallard (*Anas platyrhynchos*) ducklings also show post-hatching recognition of, and attraction to, calls heard during the late embryonic stage (Hess 1972, 1973). Bailey and Ralph (1975) found increased attraction for and movement toward sounds heard during late incubation in Ring-necked Pheasant chicks (*Phasianus colchicus*).

Semi-precocious Laughing Gull (*Larus atricilla*) chicks respond to calls of the natural parents, but not to strange parents, if the chicks have had prior experience with the calls of their parents (Beer 1970, Impekoven 1976). Early post-hatching exposure of Ring-billed Gull (*Larus delawarensis*) chicks to feeding vocalizations of adults increases recognition of individual adults (Evans 1980).

Perinatal exposure to parental calls in Common Murre (*Uria aalge*) chicks determines recognition of the parents and enhances preference for the parent-specific calls in choice tests (Tschanz 1968). However, in these studies, whether prenatal, perinatal or postnatal exposure to calls, preference and recognition was for the same sound heard during initial exposure and might be considered as associative learning (Bailey and Ralph 1975).

Incubating Ring-necked Pheasant hens vocalize throughout most of the 23-day incubation period with a variety of low-frequency, low-intensity calls. Field observations and recording of incubating hen pheasants revealed an increase in some of these calls and a decrease in others as hatch approached. The call most frequently given by incubating hens during the final week of incubation can be described as a "mew" sound of low frequency, relatively long duration and modulated downwards (Fig. 1a).

Pheasant chicks are brooded on the nest for 24 to 48 h before the hen leaves and vocalizes to the chicks, who then follow. The calls that the hen gave during incubation are replaced by other calls, which were never given during incubation. These post-hatching calls—a feeding or brood-gathering call (Fig. 1b) and caution call (Fig. 1c)—are obeyed correctly by the chicks the first time the hen gives them (Simmons 1975).

Heinz and Gysel (1970) have documented the various adult pheasant calls including feeding and caution calls. Heinz (1973) found, in the laboratory, that day-old pheasant chicks were attracted equally to the feeding call (brood gathering call) and the caution calls. However,

field-reared chicks were attracted to the hen's feeding call, but scattered and hid motionless when the hen gave the caution call (Simmons 1975).

Total obedience and correct responses by pheasant chicks on first presentation of the calls by the hen implies either that the responses are innate or that experiential factors act prenatally or perinatally to evoke the responsiveness of the chicks to specific calls. Results presented by Heinz (1973) indicate a high degree of innateness. Findings of Bailey and Ralph (1975) suggest that prenatal learning might be involved. The purpose of my study was to determine the role of the "mew" incubation call in altering sensitivity and responsiveness to the post-hatching feeding and caution calls.

MATERIALS AND METHODS

Eggs collected from a population of caged breeder pheasants of game farm origin were incubated in a forced-air automatic commercial incubator until the 17th day when they were moved to Curfew free-air incubators (model A) until hatching at 23 days. The "mew" call was played to developing embryos of experimental chicks ($n = 50$) continuously throughout the last week of incubation. The call sounds were played repeatedly on a 5-min continuous loop tape on a tape deck (Uher 4000 Report-L) through an open speaker (5-cm diameter) suspended 10 cm above the eggs. Pauses between sounds on the tape varied from 30 to 60 s. Sound level was maintained at relatively low intensity (40 dB) at egg surfaces. Eggs of control chicks ($n = 30$) were incubated with no call being played. Extraneous sounds and general white noise were not controlled but were presumed equal for both experimental and control eggs and averaged 40 dB in the open testing and incubation rooms.

The "mew" call was recorded from six incubating hens individually by an enclosed microphone (Uher M-534 dynamic microphone) suspended beside the nests. Sounds were transmitted over lines through a manually-operated switch box and recorded on tape (Uher 4000 Report-L) from an elevated blind 30 m away. To overcome line resistance, preamplifiers were installed. An observer monitored vocalizations of the incubating hens and noted behavior that occurred with the vocalizations. Sections of tape of the "mew" call with fewest extraneous sounds were transferred to continuous loops. The feeding and caution calls were recorded in part in a similar fashion. Additional recordings were made using a microphone mounted in a parabola located 10 to 20 m from the vocalizing hens. Feeding and cau-

tion calls were also transferred to continuous loop tapes.

After hatching and between testing days, groups of experimental and control chicks were held in separate rectangular cardboard enclosures placed on a paper-covered floor. Food (pheasant starter crumbles) scattered over the floor was always present. Water was available from several chick fountains within the enclosures. Heat and light were supplied by brooder lamps suspended over the enclosed area. Experimental and control chicks were treated identically until testing and during intervals between trials.

Birds were tested during the first day post-hatching (one day of age) as well as at three and five days post-hatching. Experimental and control birds were separately tested in groups of five chicks to simulate a clutch. Chicks of each five-bird test group of experimentals or controls were selected randomly from their respective populations without replacement during each test day. Between test days, chicks of experimental and control groups were replaced in their respective brooding pens. Testing on the three test days was on the same birds but test groups were not necessarily composed of the same individuals. One-half of the experimental birds were tested for responsiveness to the feed call (Fib. 1b) and one-half to the caution call (Fig. 1c) on each given test day. Control chicks were treated similarly with one-half the birds tested on the feeding call and one-half on the caution call on any given test day.

Because previous work by Heinz (1973) on responsiveness of pheasant chicks to various pheasant vocalizations had been conducted using individual birds instead of groups, chicks from one hatching ($n = 40$) were tested individually rather than in groups of five. Otherwise, all procedures were identical.

As an added control, one group of hatchlings ($n = 40$) was tested on the "mew" incubation call. Experimental chicks ($n = 20$) heard this call during the last week of incubation, while controls ($n = 20$) were incubated in silence. These birds were compared for the positive response of moving to the "mew" call only with no testing for responses to feeding or caution calls.

All testing was conducted in a rectangular chamber ($2.00 \times 0.50 \times 0.25$ m) lined throughout with burlap and uniformly heated by infrared brooder heat lamps. Identical tape recorders (Uher 4000 Report-L) protruded 3 cm into each end of the chamber. The call on which a given group of chicks was to be tested was presented from one of the tape recorders, the other was silent during testing any single
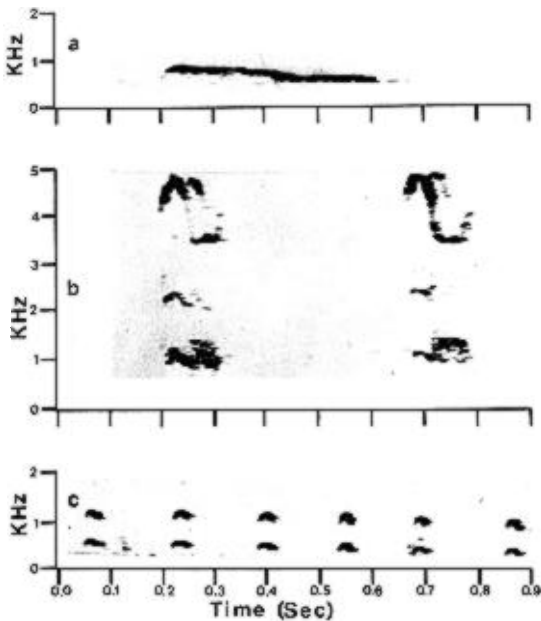
FIGURE 1. Sonographic representations with frequency and duration of hen pheasant calls: (a) "mew" incubation call; (b) feeding call; (c) caution call.

TABLE 1. Regression analysis and comparisons of positive responses and slopes of pheasant chicks over test time between control (C) and experimental (E) birds at one, three and five days post-hatching. Tested on feeding, caution and "mew" incubation calls.

Call	Group	r^2	Z comparison of correlations	t-value
Day 1				
Caution	C	.958		
	E	.841	1.22	0.22
Feeding	C	.693		
	E	.464	0.63	1.10[a]
Day 3				
Caution	C	.415		
	E	.885	1.70[b]	1.23[a]
Feeding	C	.407		
	E	.398	0.02	1.12[a]
Day 5				
Caution	C	.786		
	E	.860	0.42	0.82
Feeding	C	.142		
	E	.691	1.70[b]	3.51[b]
Combined (Days 1, 3 and 5)				
Caution	C	.929		
	E	.990	0.33	—[c]
Feeding	C	.751		
	E	.778	0.11	—[c]
"mew" incubation	C	.673		
	E	.918	1.32	—[c]

[a] $0.15 > P > 0.10$.
[b] $P > 0.05$.
[c] Slope comparisons not calculated for combined days.

test group. The chamber floor was divided into three sections of equal size. Movement into the section at the sound end was considered a positive response, movement to the silent end was assessed as negative, and movement in or returning to the center section was considered as neutral. A small amount of food (pheasant starter crumbles) was sprinkled in each of the end sections of the chamber, but none in the center, neutral section.

Each group of five birds was held under a release box in the center of the chamber for 1 min before the test call was started on one of the tape recorders. The chicks were released by lifting the box coincidentally with the start of the call. The call was presented intermittently but continuously throughout each 10-min test. Intensity of test calls at the release point was approximately constant at 45 dB (± 3 dB) for both calls, from either source location and across tests.

Each test consisted of instantaneous total scan observations made at nine predetermined times (0.5, 1.0, 1.5, 2.0, 3.0, 4.0, 5.0, 7.0 and 10.0 min elapsed time) over the 10-min test period. Location and behavior of each bird were recorded for each observation time. Attraction strength of the call was determined by the number of birds in each section of the test chamber at each observation time and at the end of the 10-min observation period.

Behavioral response to a given call was indicated by the number of birds per observation interval displaying the proper response to the call heard; pecking at food or other objects in response to the feeding call, and fear crouch (intense flat crouch posture usually with neck extended and head on floor of chamber) in response to the caution call.

Responsiveness of birds over the test period was subjected to regression analysis (Kleinbaum and Kupper 1978). Statistical (t-test) comparisons of slopes were made for age and call. Comparisons of experimental with control birds for positive response at end of test period and for correctness of behavior also were made with t-tests (Steel and Torrie 1960).

RESULTS

Attraction to the caution call in one-day-old birds was greater in experimentals than in controls over the whole test period. Correlation coefficients and slopes were not significantly different ($P > 0.05$). Responses to the feeding call were initially higher in experimentals than in controls but became gradually more similar during the 10-min tests. Correlation coeffi-
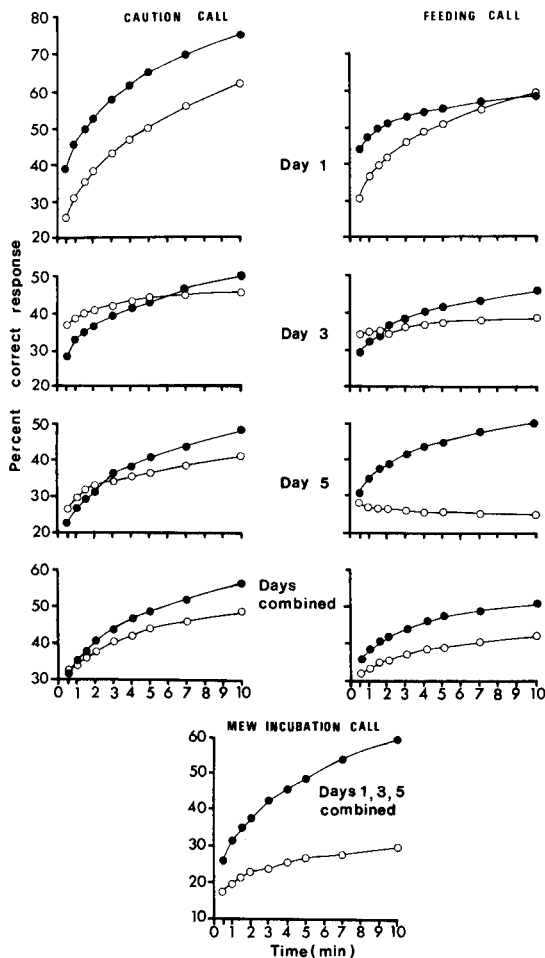
FIGURE 2. Fitted curves for correct positive response for all test times for experimental and control chicks evaluated on caution, feeding and "mew" incubation calls at each test age. Curve solved as linear regression follows formula: $\ln y = b \ln X + \ln a$.

TABLE 2. Percent of pheasant chicks responding by moving to and remaining at feeding and caution calls at end of 10-min test as compared to chance.

Age (days)	Test call	Experimentals		Controls	
		Percent positive	Chance comparison (*t*-value)	Percent positive	Chance comparison (*t*-value)
1	Feeding	60	2.26[a]	50	1.00
	Caution	84	4.37[a]	55	0.99
3	Feeding	53	1.29	34	0.11
	Caution	60	4.05[a]	44	1.47
5	Feeding	56	1.97[a]	26	1.26
	Caution	49	0.93	40	0.33

[a] $P < 0.05$, $t > 1.77$, one-tailed test.

were similar ($P > 0.05$). Responses to the feeding call were greater in experimentals than in controls at the beginning of testing and differences increased over the test period. Correlations were significantly different ($P < 0.05$); slopes were also significantly different ($P < 0.05$; Table 1 and Fig. 2).

Responses for birds of all three age groups combined were generally higher for experimental birds than for controls, but there was no difference between correlation coefficients ($P > 0.05$; Table 1 and Fig. 2).

One group of chicks was tested at one, three and five days post-hatching for attractiveness of the "mew" incubation call. Experimentals responded positively to this call to a higher degree than did controls, but correlation coefficients were similar ($P > 0.05$). Responsiveness in these birds was similar to that of birds tested on the feeding and caution calls at the same ages (Table 1, Fig. 2).

Because responses were not maximal immediately but increased in a curvilinear fashion over the 10-min test, responses of birds were compared with chance expectations for positive location at the end of the test period. Chance expectation in this situation would be 0.33 for each section in this test chamber after birds moved. At release, bias would favor the center (neutral) section because it is the release site. Once having moved and possessing further mobility, probability of being in any one of the three sections would be equal.

Positive response to the feeding call by experimental chicks was significantly greater ($P < 0.05$) than expected by chance at one and five days post-hatching. Positive response of controls to the feeding call did not differ from chance (Table 2). Control chicks tended to remain in the neutral area at one day of age and moved to the negative at five days of age.

Attraction of the caution call was significantly greater ($P < 0.05$) than chance expectations in experimentals at one and three days

cients ($P > 0.05$) and slopes ($0.15 > P > 0.10$) were not different (Table 1, Fig. 2).

At three days, control birds responded to the caution call at a higher level initially. However, experimentals responded positively by moving toward the sound source more than controls after the midpoint in the tests. Correlation coefficients were significant ($P < 0.05$), slopes were not different ($0.15 > P > 0.10$). Responses to the feeding call had the same pattern as to the caution call with experimentals starting lower but ending higher than controls during the tests. Correlation coefficients were similar ($P < 0.05$) and the slopes were not different ($0.15 > P > 0.10$; Table 1 and Fig. 2).

Responses to the caution call in five-day-old birds resembled those of three-day-old birds, but comparisons of slopes and correlation coefficients between experimentals and controls

TABLE 3. Percent of chick-observations of correct behavioral response to presented calls. Experimental chicks had been exposed to hen incubation call prior to hatching, control birds were incubated in silence.

Age (days)	Correct responses to feed call				Correct responses to caution call			
	Control[a]	Experimental	t-value[b]	P	Control	Experimental	t-value	P
1	9.0	21.8	−2.33	<0.05	11.7	0	+3.22	<0.01
3	15.0	18.2	−0.74	<0.25	12.7	44.6	−2.49	<0.02
5	14.0	17.8	−1.14	<0.15	10.3	10.6	−0.61	<0.30
Average	12.8	19.4	−4.81	<0.01	11.6	18.4	−2.28	<0.02

[a] Three control groups and five experimental groups tested on each day. Each group composed of five individual birds.
[b] One-tailed t-test. Arcsine transformation of percentages was used in statistical analysis.

post-hatching and was not different from chance in the controls ($P > 0.05$). Experimentals showed a much greater affinity for the caution call at one day of age than at three or five days of age (Table 2).

Feeding and feeding-like behavior in response to the feeding call were shown most by experimental chicks at one day of age. When tests at three days and five days post-hatching were combined with the one day post-hatching tests, the experimentals showed significantly more correct responses to the feeding call than controls (Table 3).

The fear crouch posture was given more in response to the caution call by control chicks than experimentals at one day of age ($P < 0.01$). However, at three days post-hatching, experimentals showed a great increase in correct responses while controls remained nearly the same as on day 1. Crouch responses to the caution call occurred significantly more in experimentals ($P < 0.05$) than controls at three days post-hatching and significantly more ($P < 0.025$) when all three test ages were combined. On the first day after hatching chicks were attracted to the caution call similarly to the way they responded to the feeding call. But at three days post-hatching the caution call evoked the fear crouch (Table 3).

Those birds tested individually rather than in groups of five showed attraction for feeding and caution calls on day 1 similar to birds tested in groups on day 1. However, on days 3 and 5 most birds either sat at the release point or walked about giving distress calls. These single birds seldom responded by feeding or pecking in response to the feed calls and never responded to the caution calls with a fear crouch.

DISCUSSION

Hatchling pheasant chicks up to three weeks old were attracted to sounds such as the cock feeding call and hen alarm call if these calls were heard during the late stages of incubation. Associative learning acting retroactively was postulated as a reason for this affinity (Bailey and Ralph 1975). Response of chicks tested on the "mew" call can be explained similarly in that the "mew" calls heard during the late stages of incubation were associated with the relative comfort during late stages of incubation. When heard after hatching, this call acted as an attractant and chicks went toward it seeking previously associated comfort.

Pheasant chicks exposed to the "mew" call during late embryonic development responded positively by approaching the feeding call and caution call more than control birds, which had no exposure to this incubation call. This greater attraction for both feeding and caution calls in experimental birds cannot be ascribed to associative learning alone because the chicks had not heard these calls prior to hatching. The differential responses in experimental and control chicks indicates that the "mew" incubation call might act to sensitize the chicks to calls heard for the first time after hatching.

However, some degree of stimulus generalization could be expected in associative learning, so attraction responses to feeding and caution calls might be generalized responses from prior associations formed with the "mew" call. The large differences in both frequency and duration between the "mew" call and either the feeding or caution calls (Fig. 1) limit this possibility. The downward modulation of individual tones of feeding and caution calls is vaguely similar, but there is a much more gradual downward modulation in the incubation call. Recognition of calls in Wood Ducks because of downward modulation and not frequency or duration has been shown by Gottlieb (1974). If modulation of the sounds rather than frequency and duration were the important feature of call recognition in the pheasant chicks, generalization might be more important than overall dissimilarities in the calls.

Responses to both the feeding call and caution call on the first day post-hatching are similar to results presented by Heinz (1973). But, at this early stage, chicks in the wild are still being brooded on the nest (Simmons 1975). Attraction to calls by the hen would be highly

adaptive until exodus from the nest. However, once away from the nest, on the second or third day after hatching, immediate crouching and hiding would be the adaptive responses to the caution call. Running to the hen when the caution calls were given would presumably attract attention and be maladaptive. However, attraction to a hen giving a feeding call would be adaptive when chicks were any age. Chicks should respond differently to the caution and feeding calls after exodus from the nest, but differing responses should not occur prior to nest exodus, only after.

Experimental chicks responded correctly significantly more often than controls by approaching the feeding call and by their feeding or feeding-like responses. Similarly, experimental chicks responded to the caution call by assuming the fear crouch posture more often than controls after one day of age and especially at three days. Feeding response and fear crouch response to the appropriate calls demonstrate increased recognition of the meaning of the calls as well as sensitization to them.

The apparent change of response to the caution call from day 1 to day 3 post-hatching for both the attraction and behavioral responses suggests that stage of development of hatchlings might have a modifying effect. Responses during the first day post-hatching are generalized, so all hen calls have an attraction function. At the time when chicks leave the nest, they discriminate between the hen feeding and caution calls. In consequence, they respond correctly with attraction to the feeding call and hiding motionless when hearing the caution call. The timing of this change of response corresponds to the changes in behavior of the hens in the field situation where hens during the early brooding stages stayed on the nest, kept chicks covered and vigorously defended or even attacked when approached. After leading chicks from the nest site, hens responded to approaching danger by giving caution or alarm calls and either running or, on occasion, flying away. The chicks invariably responded by crouching motionless and hidden until the hen returned to reassemble the brood (Simmons 1975). In both field and laboratory situations the type of response evoked by the caution call changes after day 1 post-hatching.

Apparent waning of responses to the caution call at five days of age might be expected during the test procedure because habituation would occur after prolonged and repeated exposure to the caution call stimulus with no reinforcement. Responses to the feeding call would not be at a high level during the tests because the chicks had continuous access to food and water between test days, so hunger drive was probably at a low level. Feeding motivation was presumably equal in all chicks, yet the feeding call increased feeding responses in experimental chicks to a greater degree than in controls. This differential responsiveness to the feeding call was especially evident by five days post-hatching.

Chicks tested in groups of five would be expected to show social facilitation in responses to both caution and feeding calls. Presumably this social influence would be especially prevalent because all birds were together prior to testing and between testing days. A wild brood of pheasants would be exposed also to sibling influences and presumably social facilitation would play a role in responses of wild pheasant chicks. However, experimental and control birds were treated identically except for exposure of experimentals to the hen incubation call. The potential social influences of siblings would be the same for both experimental and control birds. Differences in responses of experimental and control chicks to the caution and feeding calls can be ascribed to the influence of the "mew" incubation call heard prior to hatching. This prehatching imprint acts either to predispose the chicks for correct responses to calls heard after hatching or possibly alters social attractions between chicks of the group so that social facilitation acts differentially on experimentals and controls.

Incubation calls by the hen probably act to sensitize and predispose embryonic chicks for proper responses to calls they will hear after hatching. These incubation calls enable the chicks to recognize calls post-hatching on first presentation and to behave appropriately to them. However, physical and neural development might have some modifying influences on the timing and expression of responses to post-hatching calls. Similarly learning could have some influence on timing and expression of responses. Presumably, incubation calls act as an agent of socialization in pheasant chicks and the process appears to be mostly completed before hatching occurs.

ACKNOWLEDGMENTS

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Department of Zoology, University of Guelph, Guelph, Ontario N1G 2W1, Canada. Received 31 August 1981. Final acceptance 21 June 1982.

RECENT PUBLICATIONS

A comparative study of the appendicular musculature of penguins (Aves: Sphenisciformes).—Donald O. Schreiweis. 1982. Smithsonian Contributions to Zoology No. 341, Smithsonian Institution Press, Washington, DC. Paper cover. 46 p. No price given. The appendicular muscles of penguins have long been investigated, yet this report is the first to be based on a family-wide study. Using the Crested Penguin (*Eudyptes pachyrhynchus*) as a type, each of the wing and leg muscles is carefully described and then compared with the condition in the five other genera. These accounts are illustrated with many anatomical drawings. Numerical analysis of the data is found to support the present classification within the order. The findings will interest systematists and students of locomotor morphology.

The Fossil Vertebrate Record of Australasia.—Edited by P. V. Rich and E. M. Thompson. 1982. Privately published. 759 p. $Aust. 20.00. Source: Dr. P. V. Rich, Earth Sciences Dept., Monash Univ., Clayton, Vic., 3168, Australia. This book is the first comprehensive volume that summarizes and illustrates the fossil vertebrates of Australia, New Guinea, and New Zealand. It is largely organized taxonomically, each of the 18 chapters discussing some aspect of a particular class or order of animals. Two chapters are partly or entirely devoted to fossil birds. The volume is furnished with indexes to Australian fossil vertebrates, abstracts in four foreign languages, and maps of Australian vertebrate fossil localities.