

BEHAVIORAL DEVELOPMENT IN THE YOUNG
OF BENNETT'S WALLABY,
WALLABIA RUFOGRISEA (MARSUPIALIA: MACROPODIDAE)

Thesis for the Degree of M. S.
MICHIGAN STATE UNIVERSITY
MARGARET ELLEN DRUMMOND

1971



ABSTRACT

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By

Margaret Ellen Drummond

The subjects of this study were two male and two female young Bennett's wallabies, Wallabia rufogrisea frutica, a Tasmanian subspecies. These were observed for ten weeks, for twenty minutes per day per young for five days a week. Each twenty minute observation period was divided into five-second time bins and the behavior observed in each bin was recorded. Types and frequencies of behavior were determined from these data. The transition from the young's dependence on the mother to independence occurs in three stages: 1) the young is completely confined within the pouch; 2) the young emerges from the pouch for short periods but stays close to the female; 3) the young is always out of the pouch and is only with the female when nursing. The only sort of maternal behavior observed occurs during the second stage of independence; the female calls to her young to return to the pouch if it is out. After permanent pouch emergence the young engage in social interactions with other wallabies and generally exhibit adult-type behaviors. Sex roles are differentiated at pouch emergence. It is postulated that "behavioral birth" occurs at pouch emergence and makes the wallaby comparable to large eutherian grazing mammals in that wallaby young are precocial at pouch emergence and hence equivalent to ungulate young which are precocial at birth. The long, intimate association between the wallaby mother and her young does not appear to entail much learning and

behavioral interaction, as it does in a eutherian with protracted infancy, such as a primate.

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A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Zoology

1971

In memory of the late Heine and Baby

ACKNOWLEDGMENTS

I wish to thank Dr. J. I. Johnson for his patient help and encouragement throughout this study. Also I appreciate the assistance in observing the animals of Michael Jaeger, Ripalda Krasnoborski, John Benson, and M. John Dwyer.

The original colony animals were obtained through the kind cooperation of the Animals and Birds Protection Board of Tasmania.

This research was supported by NIH Research Grant NS 05982, NIH Training Grant GM 01751, and NIH Facilities Grant IP06-FR0036.

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INTRODUCTION

The marsupial mechanism of reproduction enforces a different mother-infant relationship than that of eutherian mammals. The marsupial young is born in a highly embryonic state and must complete its development contained within the female's pouch. Thus the mother and her young have an extended period of close association before the young becomes independent. Although much of the marsupial work in the literature has centered on reproduction, this being an area of most striking difference between marsupials and placental mammals; very little work has been done on maternal behavior and the ontogeny of behavior in the young. Most behavioral information found in the literature is largely anecdotal and is incidental to studies on some other aspect of marsupial biology.

Beach (1939) made some observations on a female Marmosa cinerea (a South American didelphid marsupial) with young. He tested the female for nest building behavior and retrieving of young; the female carried strips of paper in the tail or mouth to the nest box and pushed either her own young or new-born rat pups under her so they could attach to the nipple. The young were weaned and left the mother when their eyes opened, although they returned to her if startled.

There are several studies which deal with the development of marsupial young after birth, e.g. the quokka (Waring et. al., 1955), the short-nosed bandicoot (Mackerras and Smith, 1960), the marsupial mouse (Marlow, 1961), the red kangaroo (Sharman and Calaby, 1964), and the rat kangaroo (Tyndale-Biscoe, 1968). These give information on the age of

weaning and of emergence from the pouch but deal with any other behavior of the young only incidentally and do not consider the young once it leaves its mother.

This literature does indicate that the Macropodidae, the kangaroo forms such as Bennett's wallaby, develop much more slowly than other marsupial groups. Macropod young go through a long period of transition from complete dependence on the female to complete independence, while other forms tend to be weaned and become independent as soon as they are fully furred and their eyes are open.

The lack of behavioral information is unfortunate, for Wallabia rufogrisea has considerable potential as a laboratory animal for correlative studies between neurophysiology and neuroanatomy and behavior in marsupials. It has a large brain for a marsupial, yet it is not an overly large animal to house. It is largely diurnal and apparently not averse to being observed, making it a good subject for behavioral studies. In addition, it reproduces readily in captivity.

The purpose of this study is to explore the ontogeny of behavior in a species in which this has not been studied. This species is a representative of an entire order in which this area has not been investigated. An attempt will be made to find parallels and differences with the ontogenetic behavior patterns observed for eutherian mammals.

METHODS

Subjects

The subjects were Bennett's wallaby, the Tasmanian race of the red-necked wallaby, with the subspecific name of Wallabia rufogrisea frutica. When this study was made, the Michigan State University population of these animals consisted of four adult males, four adult females, and four young. Two of the females - Hal (Bruce's mother) and Ida (Baby's mother) - arrived from Tasmania in October of 1968. Del (Esther's mother) was born at Michigan State in the spring of 1967, and May (Heine's mother) was born here in the spring of 1969. The two females from Tasmania are believed also to have been born and raised in captivity.

The four young consisted of two males, Bruce and Baby, and two females, Esther and Heine. Their precise ages are unknown. A pouch check on November 6, 1969, revealed all four adult females to have a young in the pouch. No further pouch checks were made, and the histories of the young are unknown until their size made their presence obvious when observing the female. Thus it cannot be said for certain if the young seen on November 6 were the same ones later studied, or if any of these were lost and a new young subsequently born. Size and general behavior indicated that Bruce and Esther were the eldest and about the same age, with Baby being the youngest and Heine intermediate in age.

Environment

The wallabies are housed in a 59 foot by 109 foot outdoor enclosure with access to a covered outdoor shed and an indoor stall which is heated in winter. Except in winter the grass and other plants in the yard are available as food. The animals are also provided with a mineralized salt block, water, cold tea, lettuce, apples, raw vegetables, and vitamin paste on bread sandwiches.

The enclosure is part of one of the Michigan State University veterinary barns, and there are personnel around during working hours going into the enclosure every day. The wallabies are a favorite with sightseers, and there is constant passing highway traffic as well. Thus the wallabies are exposed to a considerable amount of disturbance. It is impossible to say what effect this disturbance combined with confinement has on their normal behavior patterns.

Observations

All of the data in this study are taken from direct observations of the animals. No experimental manipulations were performed; the observations were of the animals' day-to-day pursuits. The observational technique was as follows: each mother and young pair (or each young, after independence from the mother) was observed for twenty minutes a day. Each twenty minute time period was divided into consecutive five-second time bins. The twenty minute time periods were timed with a stopwatch, and the animal's behavior during each five-second time bin was recorded in a notebook with appropriately marked spaces. The animals were observed for five days every week, resulting in a total of 100 minutes of observation per animal (or per mother-young pair) per week. The data were examined with these 100 minutes per week as the time base. Observations continued for ten weeks, from May 11 to July 21, 1970. The above technique is modified from that used by Bombardieri and Johnson (1969) for observing opossums.

Before I began the actual timed, data-taking observations, I spent about a month observing the wallabies to get generally acquainted with the types of behavior they exhibit. Thus when actual data-taking began, I had a general, yet flexible, sort of code in mind for recording observed behaviors. However the categories of behavior described in the

results section were not firmly delineated until the data were analyzed.

The observations were made in the afternoon, generally between 3:00 P.M. and 6:00 P.M. Generalizability of these afternoon observations to other times of the day was tested in the following manner. The day was divided into twelve two-hour time blocks. Over a two-week time period observations were made in each of the twelve time blocks, in randomly assorted order (modified from Bombardieri and Johnson, 1969). Regular afternoon observations were also made for six days a week for this two-week period to provide an equal time base for the comparison of the two sets of observations.

Statistical analysis indicates that behaviors observed in the afternoon are representative of behaviors observed throughout the day with respect to the kinds of behaviors observed and the amount of time spent engaged in those behaviors. This comparison will be discussed more fully in the results section.

The scores of three "second observers", each observing for one day, yielded a 96.5 per cent agreement with those of the principal observer for those days.

RESULTS

The observations obtained on the behavioral development of the young wallabies can be divided into three categories: those concerned with the transition from dependence on the mother to independence from her, those concerned with social interactions, and those concerned with the general development of adult behavior patterns.

I. The Transition from Dependence to Independence

In this category will be discussed emergence from the mother's pouch, weaning, and mother-young interactions and maternal behavior.

A. Pouch emergence

In looking at pouch emergence, three measures were used: time spent in the pouch with the head in, time spent in the pouch with the head out of the pouch, and time spent out of the pouch. To explain these categories more fully, the young while in the pouch may have various parts of the body out - the whole head, ear(s), tail, hindlimb(s), forelimb(s) - or it may be completely inside the pouch. The head in the pouch category includes the young being completely in the pouch or having any part of its body out except the whole head. Any time that the young has its whole head or its head and forearms out is recorded in the head out category.

This head in or head out dichotomy gives a measure of the amount of time the young spends attending to its external environment while it is still confined to the pouch. Since the young can generally have its head in or out at its own volition, the young animal is in a position to regulate the amount of input it receives directly from the environment. (Occasionally the female will be lying down in such a way as to occlude the pouch opening, although a really determined young could probably squirm enough to make her roll over.)

Time spent out of the pouch is self-explanatory and is probably the most accurate available measure of the development of the young's independence from the mother. (The time of weaning would be the ultimate criterion of independence, but this is very difficult to determine. The young, when out of the pouch, nurses with its head placed in the female's pouch. Once the head is in the pouch, the observer cannot determine if the young is nursing or not.)

Figure 1 shows the above three measures for each young wallaby, plotted over time. Bruce (Figure 1a) was already spending part of the

Figure 1. Frequency of Head In, Head Out, and Out of the Pouch over Time for Each Young

----- Head in
----- Head out
----- Out of the pouch

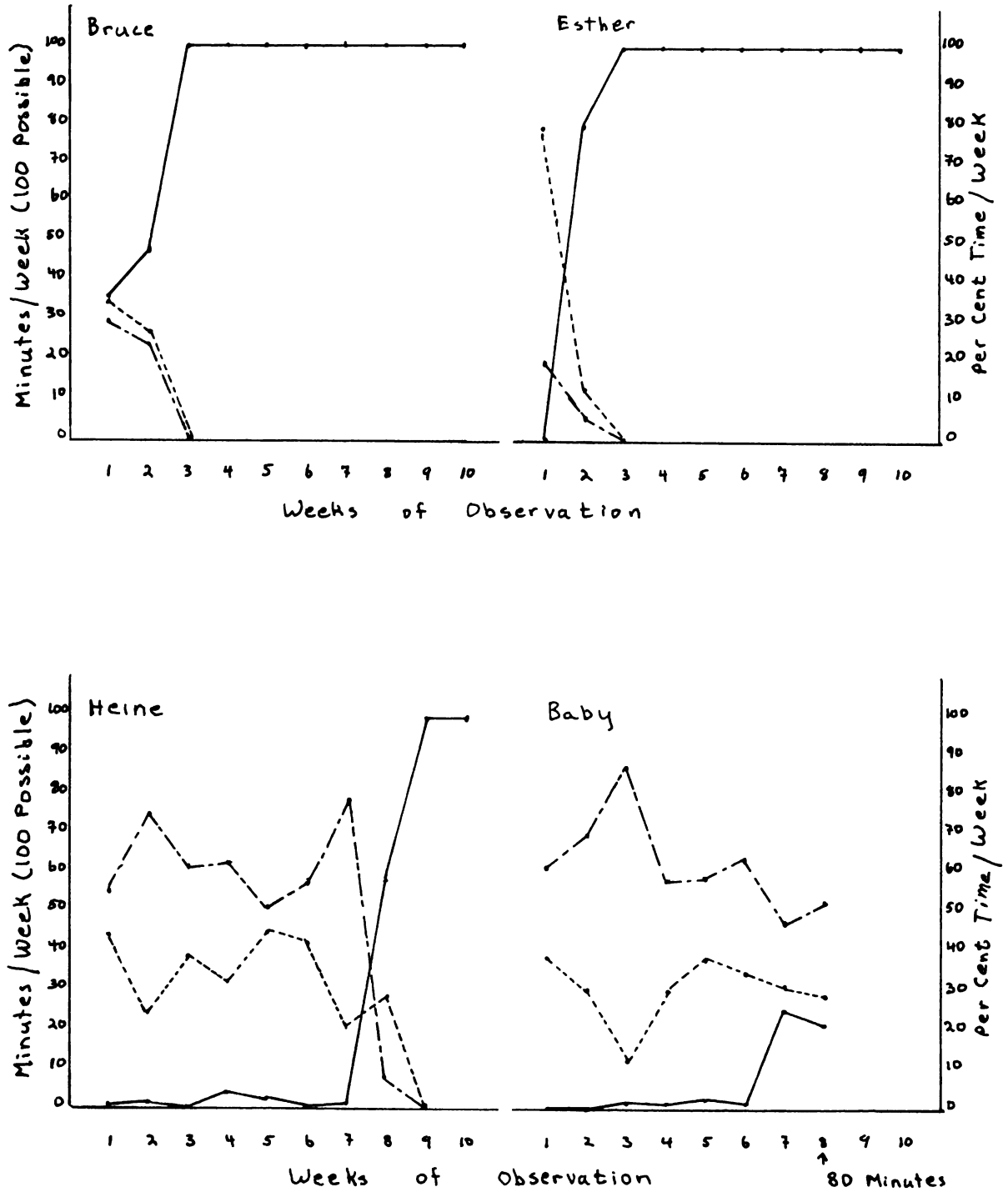


Figure 1

time out of the pouch when observations were begun. During Week 1 Bruce was out of the pouch 35 minutes of a possible 100 minutes. He was out for 48 minutes in Week 2 and from Week 3 on was never again observed to be in the pouch. The head in and head out measures for Weeks 1 and 2 are head in, 30 minutes and 24 minutes, respectively, and head out, 35 minutes and 28 minutes. These measures of course decline as a function of the increasing amount of time spent out of the pouch and drop out altogether when the young is finally out of the pouch all of the time.

Esther (Figure 1b) was not observed to be out of the pouch at all during Week 1, but was out for 80 minutes in Week 2, and was completely out from Week 3 on. This transition from always being in the pouch during Week 1 to always being out by Week 3 is even more abrupt than the graph indicates. The data point for Week 2 shows that she was out of the pouch for 80 minutes out of 100; actually she spent all 20 minutes in the pouch on day 1 and all 20 minutes out of the pouch for each of the next four days. Thus Esther's complete pouch emergence appears to have actually occurred overnight, but since it occurred in the midst of a five-day observational unit, it does not show as such on the graph.

The head in measure for Esther was 20 minutes in Week 1 and 6 minutes in Week 2. The head out times were 80 minutes in Week 1 and 14 minutes in Week 2. These measures have both dropped out by Week 3.

Heine (Figure 1c) was out of the pouch for very little time (0 to 4 minutes per week) for the first seven weeks of observation. During Week 8 she was out for 58 minutes and by Week 9 was observed to be out of the pouch all of the time. The head in and head out measures vary over the eight weeks for which they are applicable. No pattern in this variation is observable; however the head in measure is consistently higher over the first seven weeks but drops below the range of the head

out measure in Week 8. The head out measure for Week 8 is well within the range of the head out measures for Weeks 1 through 7. Of course, by Week 8, time spent out of the pouch has increased considerably, affecting the head in and head out measures.

Times for head in, head out, and out of the pouch are shown for Baby in Figure 1d. Baby was found dead on the ground in the wallaby yard on day 5 of Week 8, so his record is incomplete. Figure 1d, for this reason, shows per cent of time per week a behavior was observed, rather than the absolute amount of time, to allow for there only being 80 minutes of observation in Week 8 for Baby. These data are still comparable directly to those for the other three animals, since absolute amounts of time based on 100 minutes per week is equivalent to per cent of time.

Baby had not completely emerged from the pouch at the time of death. The cause of his death is unknown; a reasonable guess is that there was some difficulty with weaning. The possibility that this animal's behavior was not normal due to some changed condition before it died plus the fact that it died before pouch emergence make these data less informative than those for the other three young.

Baby was out of the pouch for some period of time in each of Weeks 3 through 8. Weeks 3 through 6 show a fairly constant but small amount of time spent out of the pouch (0.4 per cent to 3.2 per cent). During Weeks 7 and 8 he spent considerably more time out (26.3 per cent and 21.7 per cent). This may indicate that he was almost ready to emerge altogether from the pouch, but due to illness or general weakness did not show the rapid rise to complete emergence shown by the other young. The head in and head out measures vary over time in no particular observable pattern. The head in measure is, however, consistently higher than the head out measure.

Figure 2 shows the per cent of time spent out of the pouch for each of the four young. Heine and Esther show the transition the most cleanly. They both changed from 0.0 per cent of the time observed out of the pouch to 100 per cent of the time observed out over a two week period. The whole transition for Bruce was not observed and Baby's death cut short his record. Behaviorally, of course, there is more to pouch emergence than the change in the amount of time spent in the pouch. The behavior of the young during the transition period will be discussed in the sections on nursing and weaning, mother-young interactions, and the stages in the development of independence.

Hopefully, the amounts of time spent with the head in or the head out would have shown some consistent directional changes over time, indicating that as the animal grew older, it spent more time with its head out of the pouch, in contact with the external environment, even before it actually emerged from the pouch. Heine and Baby are the only two animals for which the head in and head out measures are recorded over a number of weeks (Figures 1c and 1d). While a greater amount of time is spent with the head in the pouch than with the head out of the pouch while the animal is still in the pouch most of the time, the variation in the two measures show no observable pattern from one week to the next. There is no indication of an increase in the amount of time spent with the head out as the time of pouch emergence approaches for either Heine or Baby.

During Week 1, the only week she was altogether in the pouch, Esther's head was out for 80 minutes and in for 20 minutes, a much higher head out time than any shown by the other three animals (Figure 1). However, nothing can be inferred from this without a record of the head in and head out measures for the preceding weeks. Likewise, as Bruce was

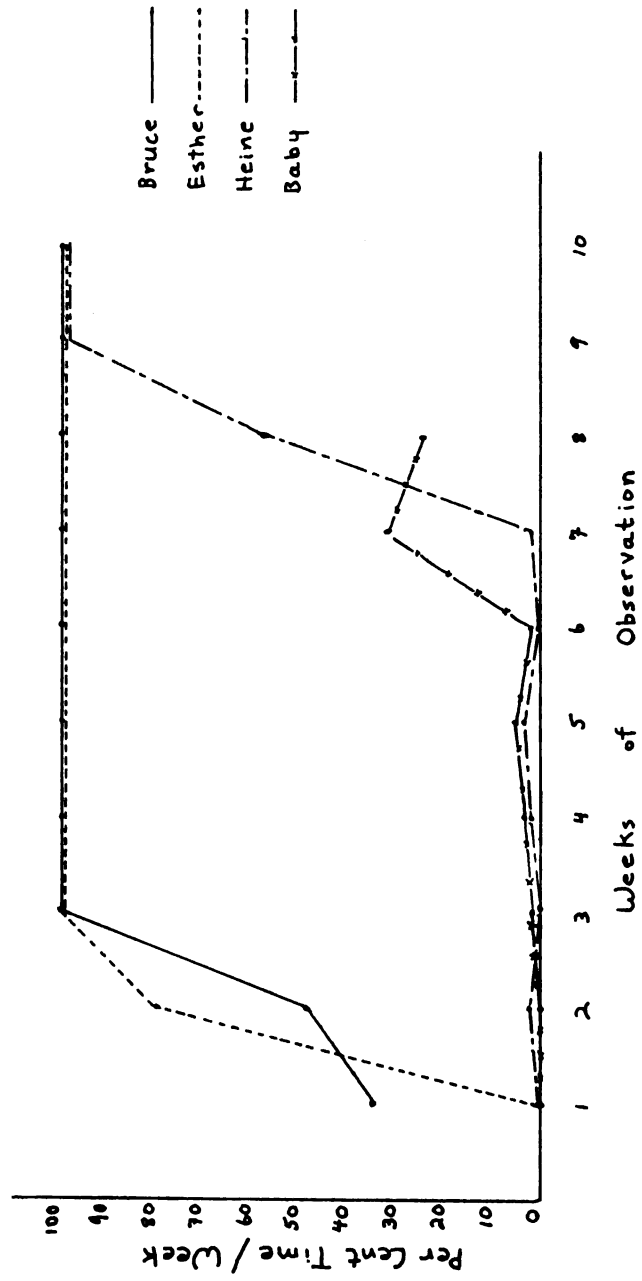


Figure 2. Per Cent of Time Spent Out of the Pouch for Each Young

already out of the pouch a good part of the time by Week 1 (Figure 1a), his head in and head out measures drop out rapidly and provide little information.

B. Nursing and weaning

Another measure of the independence of the young from the mother is the time of weaning. As mentioned above, this is difficult to determine in these animals. When the young animal is inside of the pouch, the observer cannot determine if the animal is nursing or not. Even when the animal is out of the pouch with the head inside, one cannot state positively that it is actually nursing.

The following measures were used to provide some indication of the transition from nursing to grazing: time spent grazing while in the pouch, time spent grazing while out of the pouch, and time spent nursing while out of the pouch. To elaborate, grazing consists of eating any food item in the yard - grass and the various provided foods such as oats, bread, and raw vegetables. The young wallaby can graze when it has its head out of the pouch. When it is small, its grazing is somewhat controlled by its mother; she must be standing with her forepaws on the ground for the young to be able to reach the grass from the pouch. As the young grows, he is able to stretch out far enough to reach the grass with his mouth while in the pouch even if the mother is sitting on her hindlegs, which is the more frequent stance. (The mean time spent sitting on the hindlegs is 9.67 minutes per twenty minute observation and the mean time for standing on all fours is 5.21 minutes, based on seventy observation periods of adult females.)

Young animals in the pouch were only seen to eat grass; that they were never seen eating any of the provided food is probably due more to never observing a mother with a pouch young who wanted to eat near enough

to any of the provided food for the young to reach it, rather than a lack of interest in such food by the young. Young animals out of the pouch seem to investigate anything that might be edible; various young were observed chewing on sticks, rags, paper, and a plastic ink pen, as well as eating the provided food items.

The nursing measure is actually the amount of time the young animal was observed to have its head in the pouch while the rest of the body was out of the pouch. The animal may or may not actually be suckling in this position; thus the measure may be inflated.

Figure 3 shows the time spent grazing while in the pouch, grazing while out of the pouch, and nursing, expressed as the observed probability of the behavior occurring during the amount of time per week the young animal spent in the appropriate position for it to occur.

Each of the four young shows one major peak in the time spent nursing. This peak comes in the week before pouch emergence for Bruce, in the week of emergence for Esther, and two weeks before emergence for Heine. There is a peak for Baby in the week before his death, again hinting that he was about ready to emerge from the pouch altogether at the time of his death.

It is possible that both this peak in nursing and the time of permanent pouch emergence can be used as relative age determinants for the young. The nursing peaks, from Figure 3, would indicate that Bruce is one week older than Esther, and six weeks older than Heine and Baby, who are the same age. The times of permanent pouch emergence, also marked on Figure 3, would indicate that Bruce and Esther are the same age and that both are six weeks older than Heine. These determinants agree quite well with the aforementioned subjective impression that Bruce and Esther were the eldest and about the same age and that Baby was the

Figure 3. Observed Probability of Grazing while in the Pouch, Grazing while out of the Pouch, and of Nursing for Each Young

- Nursing while out of the pouch (— indicates no time out of the pouch for that week).
- Grazing while in the pouch.
- - - - - Grazing while out of the pouch.

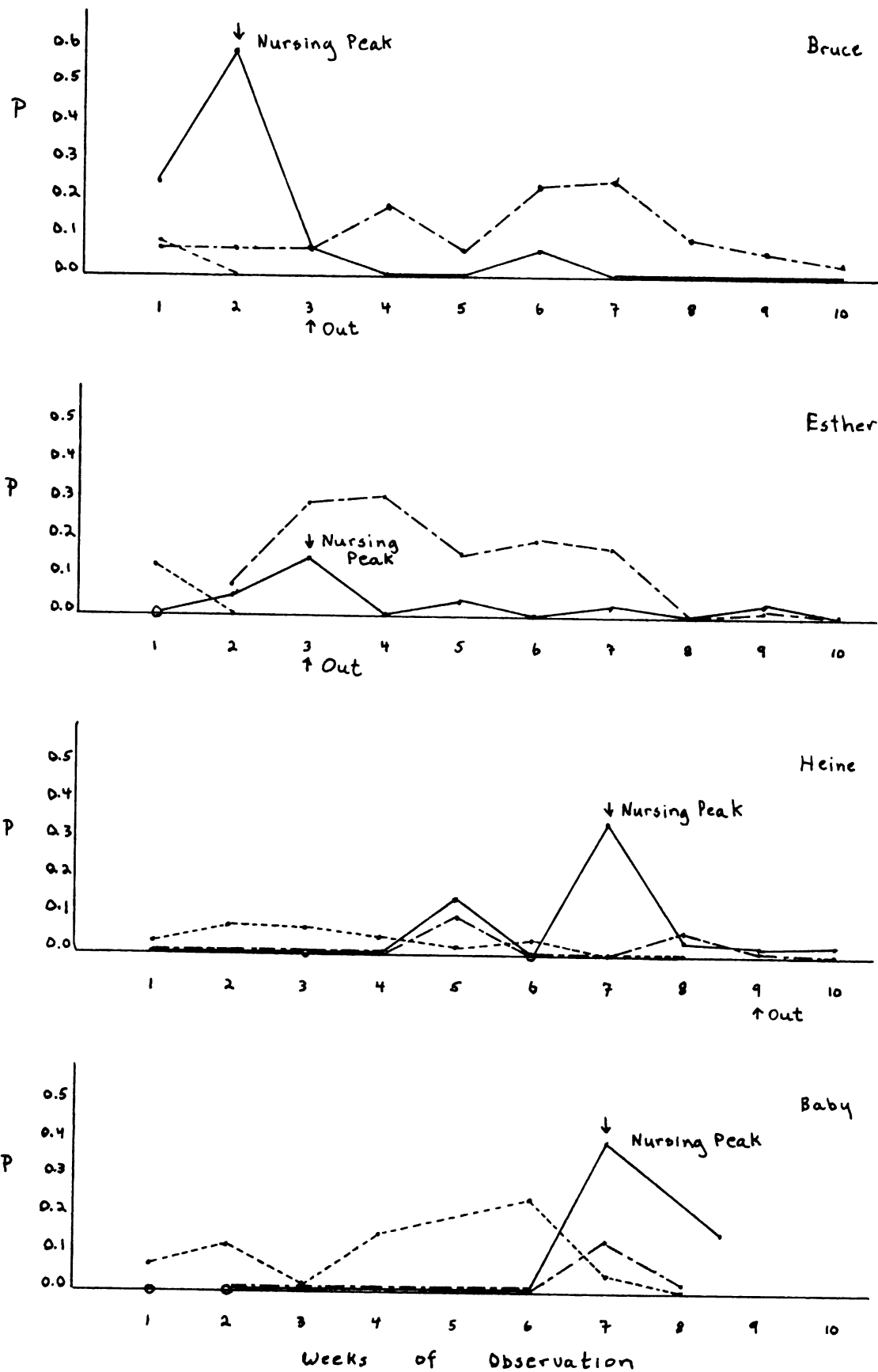


Figure 3

youngest. That Heine looked to be older than Baby may have been due to Baby being weaker and not developing as fast as Heine.

The other two measures, grazing in and grazing out, are quite variable among the four animals and do not present any recognizable pattern, except that the grazing in measure drops out when the young emerges from the pouch. The decrease in the amount of grazing done by Esther in Weeks 8 through 10 ($P = 0.0$ for Weeks 8 and 10 and $P = 0.06$ for Week 9) does not necessarily indicate that she was not eating. The comparison of these data with the data for a twenty-four hour day during Weeks 7 and 8 (Table 3, page 42) showed that Esther grazed significantly more often during the twenty-four hour observations than during the regular afternoon observations. This indicates that for some reason Esther has a pattern of eating different from that of Bruce at least. Rather than nibbling throughout the day, she may concentrate her eating at one time of day.

C. Mother-young interactions

A third way to approach the development of independence in the young wallaby is to look at the interactions between the mother and her young and at her maternal behavior, such as it is. Due to the long and intimate physical relationship which exists between a marsupial mother and her young after birth, especially among the macropods, one might expect more behavioral interaction between mother and young than one actually finds.

Before the young emerges from the pouch at all and after it is out of the pouch all of the time, the mother generally ignores her offspring. While the young is in the pouch with its head out, the female may lick it on the head while she is grooming herself around the pouch area. This relationship in time between grooming herself and licking her young

suggests that she may be grooming the young as an extension of her own body. Occasionally the female may lick the young while it is near her while out of the pouch. The wallabies also scratch themselves as a grooming activity, but no female was ever observed to scratch her young.

After the young is permanently out of the pouch and no longer with the mother, the mother and her young may sniff and paw at one another when they happen to meet. Sniffing and pawing are characteristic patterns of interaction between any two adult and/or independent juvenile wallabies. The female and her offspring appear to be interacting as two unrelated animals; there is no special mother-young character to this behavior.

One very interesting pattern of maternal behavior and mother-young interaction does occur during the transition period, when the young is coming out of the pouch for short periods of time and generally stays quite close to the mother. Occasionally during this period, when the young is out of the pouch, the female will emit a characteristic call and the young will return to the female and climb back into the pouch. The call is a double clucking sort of noise, sounding as if the female were clicking her tongue against the roof of her mouth rapidly twice in succession. To my ears, I can imitate her sound by doing just that, and once got Bruce to attend to my clucking at him. (This was after he had been completely out of the pouch for some weeks.) The female wallaby's cluck is, however, much louder than mine.

This behavior on the part of the mother is variable among the four females. In the two weeks Bruce was out of the pouch part of the time, his mother called to him six times while he was out. Five times he returned to the pouch and the sixth time he approached his mother and put his head in the pouch without getting in. Once he returned to the pouch

without a detectable signal from the female.

Once Esther was first seen out of the pouch, she was not again observed to be in the pouch. Her mother was never heard to call to her, and Esther was not seen to try to re-enter the pouch. Whether the female's never calling Esther was due to Esther's rapid transition from being in the pouch to being out, or her rapid transition was due to her mother's never calling to her to return is a moot point. Anyway, among the four mother-young pairs, Esther's transition to independence is unusual, as is her mother's not calling to her.

Heine was in and out of the pouch for eight weeks before she came out permanently. During this time, her mother was heard to call twice to her. Once Heine was out and returned to the pouch. This instance was unusual in that the female clucked repeatedly for about 15 seconds before Heine re-entered the pouch and continued to cluck for 5 seconds after the young was in. Usually a female gives only one double cluck. In the second instance of her mother's calling, Heine was in the pouch with her head out and pulled her head into the pouch in a response to the female's call. This time the female gave only the usual one call. Heine was also observed to re-enter the pouch twice without a call from the mother.

Baby had been coming out of the pouch for short periods of time for six weeks before he died in the eighth week of observation. During this time he re-entered the pouch nine times in response to calls from his mother and eleven times without an observable signal from her. These high figures in comparison with those for Heine, who spent a comparable number of weeks in the pouch during observation, are perhaps due to the fact that Baby came out of the pouch more times during the transition period. Compared with Heine (Figure 2) over the first six weeks of

observation, for instance, Baby spent comparable amounts of time out of the pouch; however the amount of time per incident of being out was generally shorter for Baby. Baby averaged 0.4 minutes duration for each time out while Heine averaged 4.4 minutes duration. Baby was out thirteen times while Heine was out four times over the first six weeks of observation.

Baby's mother also showed one instance of repeated clucking in calling her young. She clucked for about 10 seconds before Baby regained the pouch, at which point she stopped clucking. Baby had immediately attended to the female's call but ran about for some time before he managed to find the female and the pouch.

Presumably the female's call is an alarm signal serving to bring the young back to the safety of the pouch when the mother has cause for alarm or sees a potential danger. However it was rarely apparent to the observer what stimulus caused the female to call to the young. Out of seventeen instances of the female calling, only three followed some sort of disturbance obvious to me. Bruce's mother called to him once as a airplane flew overhead, once as a motorcycle went by, and once as several sheep rapidly approached the fence between the wallaby yard and an adjoining pasture.

If the female is lying down, standing or grazing with the forefeet on the ground, or sitting with the tail between the legs in a resting position, and is aroused to call to her youngster, she will rise to stand on the hind legs in a more alert, attentive position. Also this posture allows the young best access to the pouch.

D. Stages in the development of independence

From the data presented on pouch emergence, weaning, and mother-young interactions, it appears that there are three periods associated

with the development of independence in the young wallaby. There is the time period during which the young does not emerge at all from the pouch, the time period when the young is out of the pouch part of the time, and the final time period in which the young is no longer in the pouch at all. There are different behavior patterns associated with each of these stages, and a description of how the young actually behaves during each stage is in order.

While the young is still in the pouch all of the time, it is presumably incapable of surviving apart from the mother, and is much more a part of her than a separate entity. Nevertheless the young is more than a passive passenger. When the young is completely within the pouch, it sometimes moves around, often quite actively, as evidenced by motions in the pouch region of the female. The movements are sometimes quite irregular, as if the young were shifting its position in the pouch; at other times they are more regular, as if the animal were scratching.

Especially as the young grows larger, various parts of the body besides the head may be out of the pouch. The tail may be hanging out, or the tail and a hind foot. Sometimes an entire hind leg is extended out of the pouch in an outstretched position. In these positions the animal must be oriented upside down in the pouch.

When the young has the head out it is generally awake, although occasionally it will be asleep or resting, with the head drooping and the eyes closed. The young can graze with the head out, cropping off the grass with its teeth. Young were not observed to manipulate food items with the forepaws while in the pouch, as adults and independent juveniles may be observed to do. The young often investigates the ground with its nose, although when the mother is on all fours grazing, it is difficult to distinguish ground-nosing from grazing in the young.

The young may have the forepaws as well as the head out of the pouch. In warm weather the wallabies often lick their forearms; these become damp with saliva and presumably help to cool the animals by evaporation. The young wallaby in the pouch will do this on a warm day; in such weather it must be especially warm inside the pouch.

The young may have the head either in or out for a considerable time, on the order of minutes, or one may pop its head in and out quite frequently. The mean duration of having the head in the pouch is 2.09 minutes and the mean duration of the head out position is 2.41 minutes, for all four young combined. The range for the head in measure is 5 seconds to 20 minutes and that for the head out measure is 5 seconds to 16 minutes 10 seconds.

It is usually impossible to recognize any event which may cause the young to withdraw the head into the pouch. One notable exception is Heine's pulling her head in as a response to her mother's cluck, as mentioned above. If the mother starts to hop while the young's head is out, the young will generally leave the head out. Sometimes the young will pull its head in as the female hops, often emerging again when the female stops. For all of the young, heads remained out 154 times as the female began to hop and were pulled in 33 times at the onset of locomotion. If the young has the head in, it will remain thus during locomotion by the female.

When the young wallaby begins to emerge from the pouch, it, of course, can exhibit a greater range of behaviors. During the period in which the young is only out of the pouch part of the time, it stays quite close to the mother. If the female moves more than a few feet, the young will follow. Very rarely during this period would one member of the mother-young pair be out of the observer's range of vision while

watching the other member of the pair. The one instance of this occurring was that Heine was not with her mother for about 4 minutes one day in Week 7, the week before she was permanently out of the pouch. During these 4 minutes Heine was inside the barn, the mother having gone into the yard. Heine was nosed and pawed by a large male; the mother then returned to the barn and Heine re-entered the pouch. The female was not heard to call to Heine, and it is indeterminable if she returned to the barn in search of her youngster.

When the young is out of the pouch, it is generally active: hopping in the vicinity of the mother on two or four feet, sniffing objects on the ground, scratching, putting its head in the pouch for brief moments. Comparisons of activity between young animals and adults will be discussed in Section III.

The young seems to fall out of the pouch rather than to climb out. The pouch opening or the pouch wall is under muscular control by the female. As she relaxes these muscles, the pouch opening enlarges and the young spills out onto the ground. The young generally gets up almost immediately from where it landed on the ground. One exception to being dumped is Bruce who was once observed to back out of the pouch by himself while his mother was lying down on her side.

The young re-enters the pouch by climbing in head first. Actually it must sort of somersault in, as it often appears right side up with the head out very soon after it climbs into the pouch. There is no observable evidence that the female wallaby either helps or hinders the young when it tries to re-enter the pouch.

After the young is permanently out of the pouch, it spends progressively less time in the proximity of its mother. For instance, Bruce, during his first week altogether out of the pouch (Week 3), was with his

mother the first and fourth days of the week, but not the other three days. After that, except for the time spent nursing, he was not near his mother except for seemingly chance encounters. Esther, who was in the pouch the first day of Week 2 and out the other four days, was not with her mother on days 2, 3, or 5 and was not with her mother except to nurse after Week 2. Heine likewise was not with her mother except to nurse after emerging altogether from the pouch. The behavior of the young after permanent pouch emergence will be further discussed in Section III on the general development of adult behavior patterns.

II. Social Interactions

An important part of the development of a young mammal is his integration into the group. Although wallabies do form dominance hierarchies (LaFollette, 1968,1971), their social organization does not seem highly complex and the animals spend very little time interacting with one another. Even so, a developing wallaby would be expected to begin to interact with adults other than its mother, as well as with other young, at some point in its development.

Three types of social interactions among wallabies can be distinguished: aggressive, sexual, and neutral. Aggressive behavior is generally initiated by a male toward another male or toward a female. The aggressor paws the second animal about the head and shoulders and growls. The second animal generally retreats, ending the encounter. Although actual fighting does occur (LaFollette, 1968, 1971), it was not observed during this study.

In sexual interactions, the male is again the initiator, approaching adult females and the young of both sexes. Sexual interactions are characterized by several behaviors in the male, any or all of which may be present during an interaction. The male snakes his tail back and forth

on the ground and noses the female's vaginal opening (or the anal region in a young male). The male may nose the female from behind at the base of her tail or may nose her from the front. For this reason it is often difficult to determine if the male is nosing the pouch region or the vaginal area of the female. The male may clasp the second animal from behind around the shoulders or the rump, in an attempt to mount. The male has the penis everted.

Copulation was never observed. Male advances were vigorously rebuffed: adult females growled and pawed (an aggressive pattern) at males who approached them sexually. Sometimes the male retreated; sometimes he persisted and it was the female who left. In general, young wallabies simply retreated from the male. Males were more persistent in sexual interactions than in aggressive ones. A male often pursued a female or a young for several encounter-retreat sequences.

The estrous cycle for Wallabia rufogrisea is given as 30 to 31 days in length (Sharman, Calaby, and Poole, 1965). No attempts were made to determine estrous cycles in the present group of animals. However one incident is noteworthy here: just two days before Esther was permanently out of the pouch, three of the adult males spent almost an entire observation period in pursuit of the mother (with Esther remaining in the pouch). The female was not at all interested and kept running from the males. Perhaps she was coming into estrus at this time; although she was behaviorally unreceptive, the males were definitely attracted to her. There is evidence that in some macropods, at least, the time of pouch emergence by the young is related to the reproductive cycle of the female. The exact nature of this relationship has not yet been determined for W. rufogrisea.

Neutral interactions are a nose-to-nose type of encounter, or some

variation of this. The basic encounter consists of two animals putting their noses together in sort of an Eskimo kiss. This may serve a similar function - identification and recognition - as the kiss described by King (1955) for the black-tailed prairie dog, Cynomys ludovicianus, and by Rood (1970) for the desert cavy, Microcavia australis. In the wallaby, this is often a mutual behavior; it cannot be observed which animal initiates the contact. Sometimes one animal definitely noses toward another; the other may respond by nosing back or may not react at all. Sometimes two animals nose toward one another without making nasal contact; they may be up to two feet apart and do this. This does appear to be a greeting or recognition interaction; it is termed neutral because it generally arouses no aggressive or retreat response as do the other two categories of interaction described.

Not all instances of contact between animals can be termed social interactions. The animals may graze, lie, or stand in very close proximity without seeming aware of one another's presence. A moving animal may brush or bump another in passing, with no response from the animal being touched.

Despite the fact that three categories of interaction can be defined, it is often difficult to determine precisely into which category an observed interaction should be placed. Therefore some of the interactions observed may have been misclassified, but hopefully any trends and conclusions are still valid.

Including social-type interactions with his mother, Bruce was involved in 20 aggressive encounters, 6 of which he initiated, 13 of which were initiated by others, and 1 in which no aggressor could be determined. Out of 8 sexual interactions, Bruce initiated 7 and was approached once. He was also involved in 27 neutral encounters. Table 1

shows the frequencies of these three types of encounters over the ten weeks of observation. No change in frequencies is apparent after permanent pouch emergence (Week 3). There was also no observable change in frequency between being the object of aggression and being the aggressor over time.

As mentioned in the section on mother-young interactions, after permanent pouch emergence, young wallabies and their mothers seem to interact as unrelated individuals, except for nursing by the young. This is evidenced by Bruce's social interactions with his mother. Bruce initiated three aggressive encounters with his mother while she initiated two toward him. He also approached her twice sexually - sniffing her vaginal region. There were three neutral encounters between the two animals.

Bruce's behavior also hints that young males may initiate sexual interactions as soon as they begin to emerge from the pouch. Bruce was first observed out of the pouch during pilot observations at the end of March. While out he jumped at his mother's head and back in what may have been an attempt to mount.

Esther was the recipient of 12 aggressive approaches and 15 sexual approaches. She did not initiate any aggressive or sexual encounters, and was involved in 51 neutral encounters. Frequencies of these encounters over time are given in Table 2. Again there seem to be no trends which develop over time after permanent pouch emergence (Week 3), except for perhaps a decrease in interactions in Weeks 8 through 10. This parallels the decrease in eating during times of observation as described above, indicating a general lessening of activity during the afternoon period in the latter weeks of observation for Esther.

Since Bruce and Esther both emerged from the pouch at the same time and are presumably about the same age, their respective interactions with

Table 1

Frequency of Social Interactions over Time for Bruce

Weeks of Observation	Frequency of Encounters:		
	Neutral	Sexual	Aggressive
1	1	1	4
2	0	0	2
3	2	0	2
4	1	0	0
5	3	1	1
6	3	1	1
7	7	0	3
8	4	4	4
9	3	0	2
10	3	1	1
Totals	27	8	20

Table 2

Frequency of Social Interactions over Time for Esther

Weeks of Observation	Frequency of Encounters:		
	Neutral	Sexual	Aggressive
1	0	0	0
2	3	1	2
3	9	2	2
4	7	2	1
5	11	5	2
6	8	4	1
7	5	1	3
8	1	0	0
9	5	0	0
10	2	0	1
Totals	51	15	12

other animals can be compared on the basis of sex. Bruce was involved in more aggressive encounters and fewer sexual ones than Esther (Tables 1 and 2). Although usually the object of aggression, Bruce was on occasion the aggressor. Esther was always the object of aggression. Likewise, Bruce was generally the initiator of sexual approaches, while Esther was always the approached. Esther was involved in more neutral encounters than Bruce (51 for Esther to 27 for Bruce). Of these, Esther was involved in 40 encounters with males and in 11 with other females. This may indicate a sexual component to neutral interactions in that males seek to interact with a new female in the group, such as an adolescent young. Bruce was involved in 16 neutral interactions with other males and in 10 with females. Data on the frequency of neutral encounters by sex for adults would be helpful but is not available.

Heine, although emerging from the pouch much later than Bruce or Esther, was the object of 7 aggressive advances and 15 sexual ones. She was also involved in 11 neutral interactions, all of which were with males. Social encounters being fairly rare events, Baby was not out of the pouch enough to interact a great deal. He was the object of one sexual interaction and was involved in one neutral encounter. Both interactions occurred in the week before his death.

In general, then, the young are socially involved with the adult members of the group and each other when they emerge from the pouch. Age of sexual maturity for these animals is unknown, but their sex roles seem to be differentiated at the time of pouch emergence: males being involved in aggressive encounters and less frequently in sexual encounters, and females being the objects of sexual and aggressive encounters.

III. The General Development of Adult Behaviors

One way to measure the maturation of the young is to look at the amounts of time they spend engaged in selected behaviors compared with adults. Behaviors looked at in this light were grazing, locomotion, and various postural positions.

Grazing has been previously defined to include eating various provided food such as oats, vegetables, and bread, as well as actually eating the grass in the yard.

There are two means of locomotion used by the wallabies; these have been combined in measuring their frequencies. The first is hopping on the two back feet, with both feet leaving the ground simultaneously. It is the more rapid pattern and is used more for sustained locomotion. The second means, stepping, uses all four feet, the two front feet advancing together, with the hind feet then brought up to the forefeet. This is a more leisurely gait and the animal generally takes only one to three steps in a bout of stepping.

There are four stationary positions: observing, standing, the grooming position, and lying down. In the observing position, the animal stands upright on the two hind feet. It may actually seem to be observing the surroundings, turning the head from side to side and moving the ears; or it may stand motionless, seemingly oblivious. For this reason, observing is perhaps a poor designation for this category, since standing on the hind feet seems to be a resting position as well as an alert position.

In the standing position, the animal is on all fours. This is perhaps also a resting position.

In the grooming position, the animal is sitting down with its hind legs stretched out in front, and its tail between its legs, also out in

front. In this position the animal often grooms itself, scratching with its forepaws or licking and nibbling its fur. The animal may also just sit in this position. Grooming - scratching, licking, and nibbling - also occurs in the observing position.

When lying down, the animal lies on its side, with all four legs on one side of the body. Occasionally the animal will graze in this position, if there happens to be some nice grass growing next to its mouth.

The time spent engaged in the above behaviors or positions after pouch emergence for the three young which permanently emerged from the pouch was compared with the average amount of time spent in these behaviors by the females who were observed with their young until pouch emergence. A total of seventeen weeks of observation of females was used in the averages. Grazing frequency can also be compared with previous observation data on these animals (Johnson, unpubl.), but the other categories are not comparable to previous data due to differences in the definitions of categories. Unfortunately the behavior of females with large pouch young may not be entirely representative of the average behavior of the total adult population. Bruce and Esther were compared with the adult females for the eight weeks they were out of the pouch and Heine was compared for two weeks. These comparisons are shown in Figures 4 through 9.

Figure 4 shows the amount of grazing the young did in comparison with the adult females of this study as well as with data on six adults observed at the same time of day in the summer of 1967 (Johnson, unpubl.). The adult females fed an average of 17 minutes per week out of a possible 100 minutes (observed probability of grazing = 0.17). The observed probability of grazing by adults in the summer of 1967 was around 0.30 (Johnson, pers. comm.).

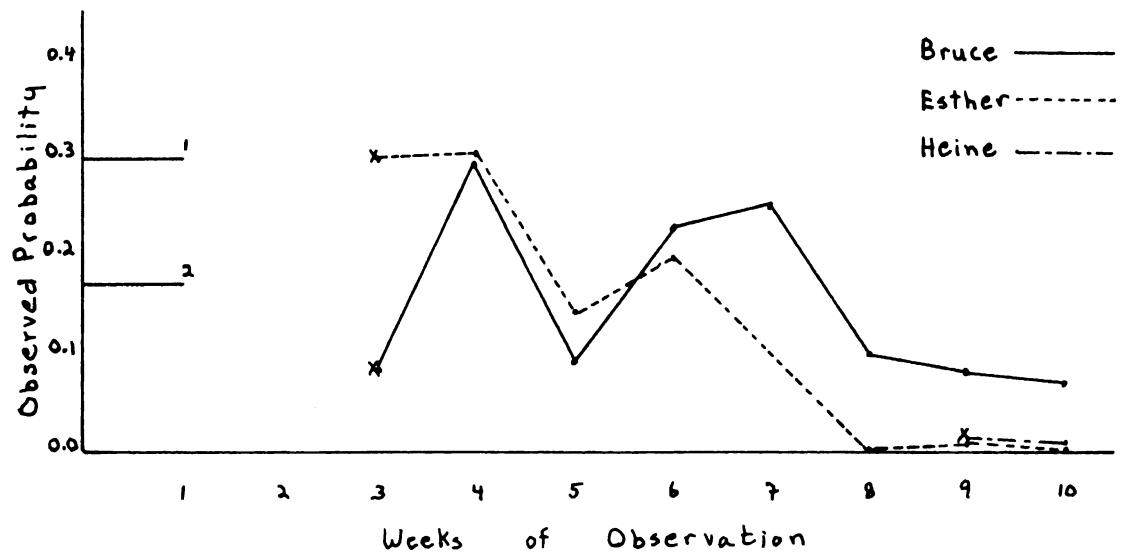


Figure 4. Frequency of Grazing over Time for Each Young Compared with Adult Females and with Adults of Both Sexes

- 1.) Observed probability of grazing by six adults in summer, 1967.
- 2.) Observed probability of grazing by four adult females in the present study.

x Indicates point of pouch emergence.

In general the amount of feeding done by Bruce and Esther fluctuates around the average of the adult females observed in this study. Both the two young and the four adult females spent less time eating than did the six adults observed in 1967. I cannot explain this difference; perhaps it is not significant. The amount of time Esther spent eating declines considerably in Weeks 8 through 10. As mentioned before, Esther seems to have a different eating schedule. Perhaps varying eating schedules among individuals account for the differences in amount of time spent feeding between 1967 and 1970.

Nursing is most frequent right around the time of pouch emergence (Figure 3); therefore one might expect the amount of grazing to be lowest at the time of pouch emergence and to increase thereafter as the amount of nursing declines. This does not seem to occur, at least for Bruce and Esther. Other than Esther's perhaps developing an eating pattern related to time of day, there seems to be no change or development in feeding behavior over time as the young animal ages.

Heine was only observed out of the pouch for two weeks; during this time however she showed very little time spent grazing. As Figure 3 shows, she also spent very little time nursing during this period. Although no comparisons were done for Heine as to time of day when behaviors occurred after pouch emergence (Table 3), it is possible that she, like Esther, ate at a different time of day.

Observed probabilities of locomotion (combined hopping and stepping) are shown in Figure 5. The probability of locomotion for adult females in this study was 0.02. Probability of locomotion for the three young is quite comparable to that of the four adult females. Locomotion is thus a relatively rare behavior for these animals.

Figures 6 and 7 show comparisons for observing and lying down

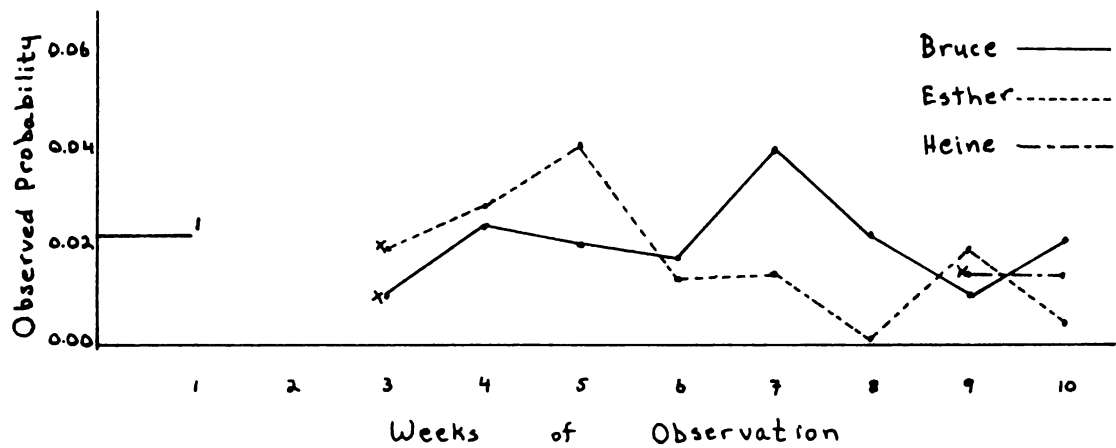


Figure 5. Frequency of Locomotion over Time for Each Young Compared with Adult Females

1.) Observed probability of locomotion by four adult females in the present study.

x Indicates point of pouch emergence.

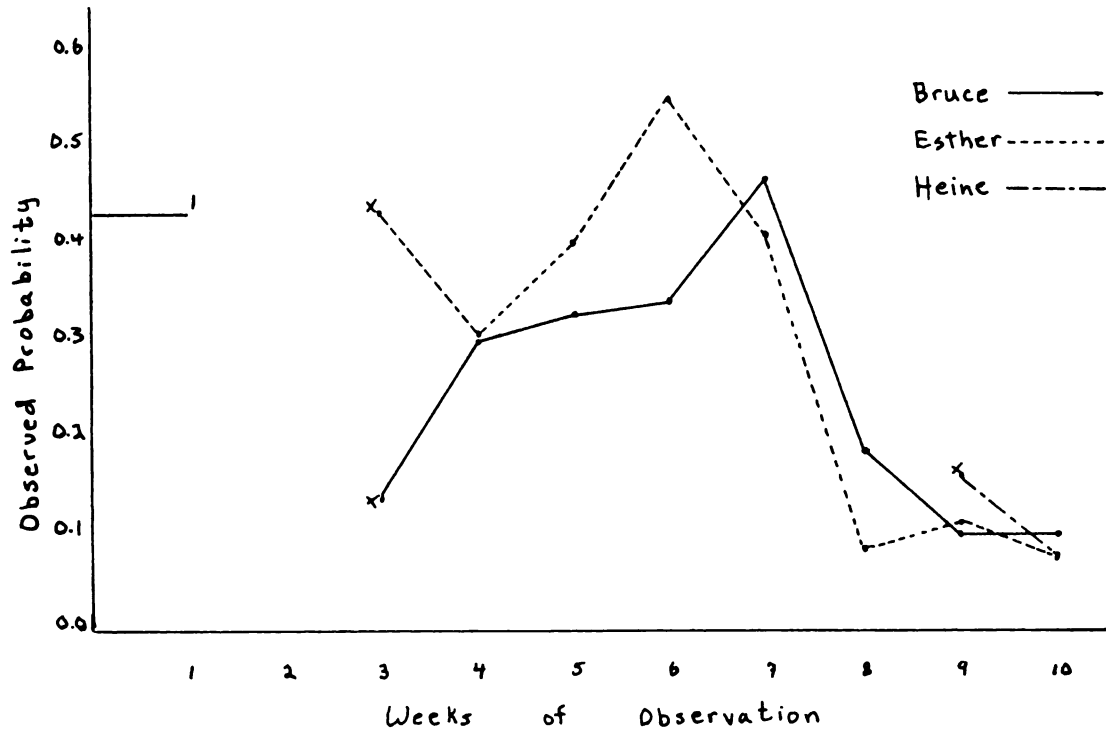


Figure 6. Frequency of Observing over Time for Each Young Compared with Adult Females

1.) Observed probability of observing by four adult females in the present study.

x Indicates point of pouch emergence.

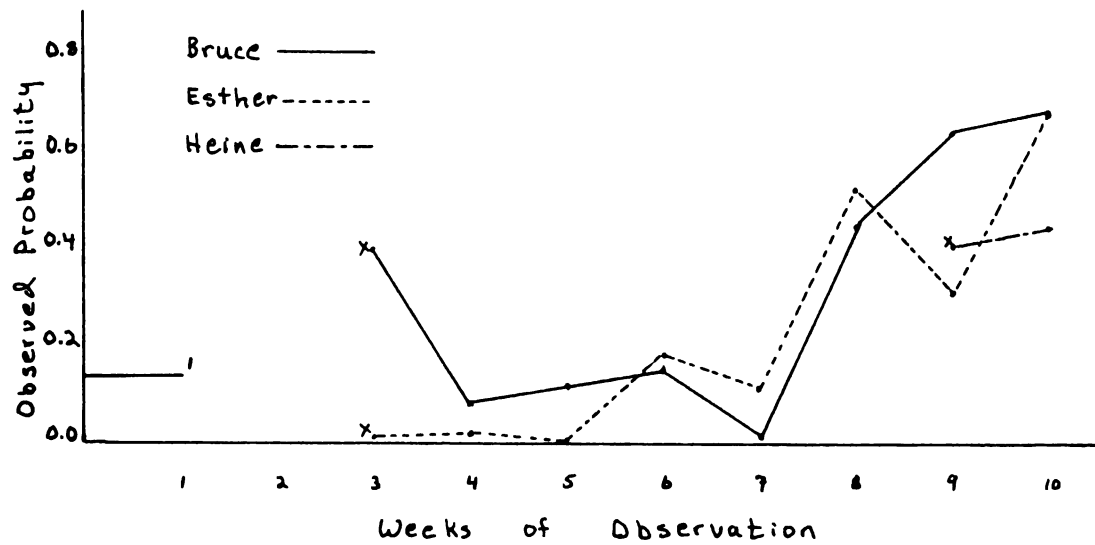


Figure 7. Frequency of Lying Down over Time for Each Young Compared with Adult Females

1.) Observed probability of lying down by four adult females in the present study.

x Indicates point of pouch emergence.

positions. For the adult females, the average probability of observing was 0.44 and of lying down was 0.14. Both Bruce and Esther show similar marked differences when compared with these figures. Through Week 7 Bruce and Esther approximate the probabilities of the behaviors occurring shown by the adult females for both observing and lying down. However after Week 7, lying down sharply increases for Bruce and Esther and observing shows a corresponding drop for the same time period.

A possible explanation for this is the weather. Weeks 8 through 10 of observation were the first three weeks of July and the weather was generally quite warm - warmer than the preceding weeks of observation. If observing is often a resting posture, and granting that lying down is such, lying down might replace observing as a function of warm weather. No adult females were observed during Weeks 8 through 10 so it cannot be determined if they showed a corresponding shift in behavior. However it was my impression that the entire group spent a great deal of time lying down on warm afternoons. Also Heine (Figures 6 and 7) shows less time observing and more time lying down than the averages for the adult females.

Comparisons for the grooming position are shown in Figure 8. Observed probability for this position in the adult females was 0.04. The three young all show much higher figures than this. Also time spent by Bruce in this position generally decreases over time, while time spent by Esther increases. Heine also spent much more time in this position during the two weeks she was out of the pouch than the average for the adult females.

Figure 9 shows standing behavior. Observed probability for this position in adult females was 0.13. All three young spent considerably less time in this position than did the adult females.

Thus, in general, the young resemble the adults more in the types

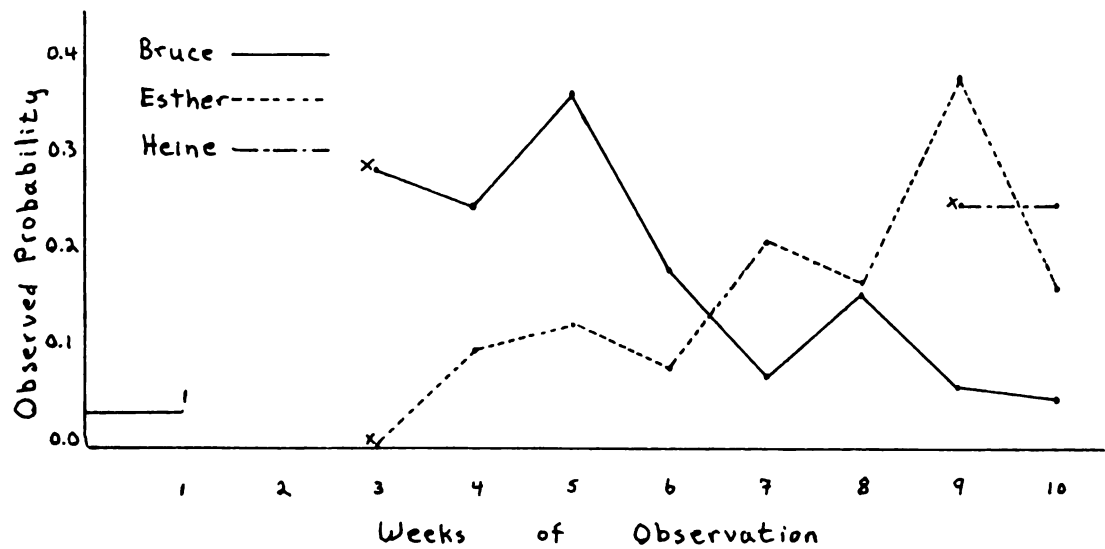


Figure 8. Frequency of Grooming over Time for Each Young Compared with Adult Females

1.) Observed probability of grooming by four adult females in the present study.

X Indicates point of pouch emergence.

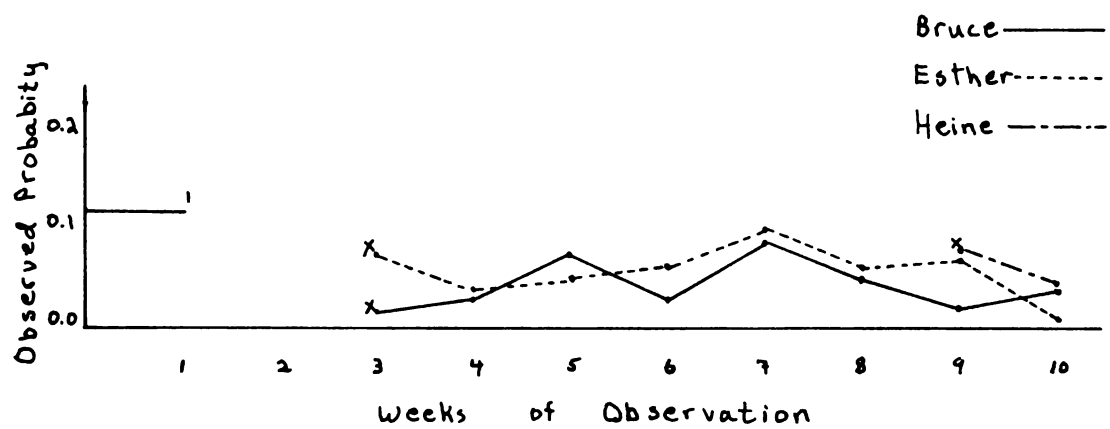


Figure 9. Frequency of Standing over Time for Each Young Compared with Adult Females

1.) Observed probability of standing by four adult females in the present study.

x Indicates point of pouch emergence.

of behavior observed rather than in the frequencies of those behaviors. Some of the differences in frequency, such as in lying down and observing, may be attributable to the weather. Others, such as standing and grooming, remain unexplained, except to say that the more time an animal spends doing one thing, the less it can spend doing another. Also, as evidenced by the grooming position frequencies for the young especially (Figure 8), individual differences may be great. Thus comparisons of highly variable individual data with an average of several animals may not be particularly useful.

It is difficult to say if any changes in behavior occur with age. Esther's feeding schedule shifted as she got older, but it cannot be said whether or not this was a function of age. Amount of time spent in the grooming position (Figure 8) changed over time for both Bruce and Esther; but since the changes were in opposite directions, they do not indicate any one directional trend over time. Standing and locomotion did not observably change over time (Figures 9 and 5). Only lying down and observing (Figures 6 and 7) show any consistent directional changes over time; as mentioned before, this may be more a function of warm weather than of changes in behavior with age. More data, especially on young and adults over the same time span, will be necessary to determine when and how the young attain adult behavior patterns.

IV. Generalizability of Afternoon Observations

Table 3 presents a statistical comparison (Student's t-test, two-tailed) of the afternoon observations with the twenty-four hour observations conducted during Weeks 7 and 8 of observation (June 22 to July 6). Different behaviors were used for some of the young since they did not exhibit the same behaviors during the two weeks due to differences in age and therefore in stage of behavioral development.

Table 3

A Comparison of the Observed Frequencies of Selected Behaviors between
the Afternoon Observations and the Twenty-four Hour Observations

Animal	Behavior	Minutes/Observation Period				S $\bar{x}$	t-value	Probability
		24 Hour	S $\bar{x}$	Afternoon				
Bruce	Observing	7.76	1.48	7.19	1.25	0.15	0.5 < p < 0.9	ns
	Grazing	4.63	1.07	3.38	0.84	0.61	0.5 < p < 0.9	ns
	Grooming	0.81	0.45	3.65	1.41	1.53	0.1 < p < 0.2	ns
	Lying Down	5.26	2.20	3.84	1.81	0.41	0.5 < p < 0.9	ns
Esther	Observing	9.37	1.46	5.45	1.58	1.00	0.2 < p < 0.4	ns
	Grazing	4.60	0.89	0.48	0.39	2.42	0.02 < p < 0.05	*
	Grooming	1.40	0.49	3.05	1.15	1.03	0.2 < p < 0.4	ns
	Lying Down	2.81	1.45	10.11	2.48	1.71	0.1 < p < 0.2	ns
Heine	Head In	9.17	2.38	8.80	2.43	0.07	0.9 < p	ns
	Head Out	3.76	1.59	4.65	1.62	0.32	0.5 < p < 0.9	ns
Baby	Head In	7.83	1.48	10.14	1.74	0.48	0.5 < p < 0.9	ns
	Head Out	8.67	1.47	5.93	1.20	0.68	0.5 < p < 0.9	ns
	Out of the Pouch	3.51	1.92	3.93	1.31	0.14	0.5 < p < 0.9	ns

ns = Not significant

* = Significant at 5% level

S $\bar{x}$ = Standard error of the mean

Degrees of freedom: Bruce df = 22

Esther df = 22

Heine df = 22

Baby df = 18

Only one behavior for one animal - grazing by Esther - showed a significant difference between the two sets of observations. Esther ate less in the afternoon than at other times of day ($0.02 < p < 0.05$). The other behaviors compared indicate that the afternoon behavior is comparable to that of the entire day.

However it is possible that observations are generalizable to the rest of the day only for Weeks 7 and 8 of observation. Data on observing and lying down for Bruce and Esther (Figures 6 and 7) indicate that the weather may influence behavior frequency. This climatic factor superimposed on a daily activity pattern may lessen the generalizability of the afternoon observations.

Nevertheless all behaviors seen in the afternoon are seen throughout the day and night and no behaviors occur at other times that do not occur in the afternoon. The variability in frequencies of behavior for each individual young from week to week in many cases also adds to the difficulty of generalizing the observations.

DISCUSSION

From the physiological standpoint, the marsupial mechanism of reproduction enforces a different mother-young relationship than that of eutherian mammals. The marsupial is born in such an undeveloped state that in essence it must undergo a period of post-partum gestation external to the mother but in close, constant association with her, attached to the nipple and contained within the pouch.

A most striking feature in the wallaby is that, for all the long period of intimate association between the mother and her young, there is a decided lack of behavioral interaction between the two animals. Except for nursing, the mother calling to her young when it is out of

the pouch during the transition period from being in the pouch to being independent is the only clearly observable example of mother-young interaction as mother and young. While the young is still in the pouch the female ignores it to all outward appearances; after it is out of the pouch permanently the young interacts with its mother in much the same way as it interacts with other members of the group.

Considering, then, that social interactions and most overt behavior occurs after pouch emergence, what might be termed "behavioral birth" occurs much later than does actual birth in the wallaby. If the time of pouch emergence can be equated with the time of actual parturition in a eutherian animal, the wallaby is quite precocial from a behavioral point of view.

This disparity between the time of actual birth and the time of "behavioral birth" is an example of the convergent adaptation of the macropod marsupial group, of which W. rufogrisea is one, with the large eutherian grazing animals. Among the eutherian hooved grazers, the young are precocial; they are able to stand and to follow the female shortly after birth, usually within a matter of hours. The macropod marsupials are large herbivores, the ecological equivalents of the large eutherian grazers; and despite the highly altricial condition of the young at birth, by the time the young is out of the pouch it is as able to keep up with the adults as is a newly born, precocial ungulate.

There are, of course, eutherian mammals which bear altricial young who subsequently remain with the female or family group for an extended time before they are able to be independent. In primates, especially, the young is helpless at birth and remains in close association with the mother for a long time. As might be expected from the above hypothesis that the macropods have converted essentially altricial young

into essentially precocial ones to meet conditions imposed by their ecological situation, the long close association between a wallaby mother and her young serves a different purpose than that association between a primate mother-young pair.

There are both advantages and disadvantages to a long period of development for a young animal. Undoubtedly, for such a pattern to have arisen, the advantages must outweigh the disadvantages. The main disadvantage to a long period of relative helplessness and dependence by the young is that the young is vulnerable to predators and accidents with which it is not yet able to cope for that long period. This disadvantage would generally be true for any animal, including both primates and macropod marsupials.

Much of a primate's behavioral repertoire and social skill is learned; the advantage of a prolonged infancy and adolescence is that it provides time for this learning to occur. There seems to be little learning involved in the behavioral development of a young wallaby; the advantage of the long association with the female is physical rather than psychological. The young remains in the pouch protected by the mother until it is large enough and strong enough to take care of itself. Thus despite an extended intimate association between mother and young in both primates and macropods, the former has a behaviorally active relationship providing information transfer from the mother to the young as well as protection; while the latter pair is quite lacking in behavioral interaction, the young marsupial receiving little more than protection and food.

Calling

There is some mention in the literature of calling by the female among macropods. These reports also indicate that the young may call to

the mother when the two are separated, but this was not observed in our W. rufogrisea. Sharman and Calaby, 1964, and Frith and Calaby, 1969, (page 68) reported for the red kangaroo, Megaleia rufa, that the young makes a "hissing squeek" when it has strayed too far from the mother and is actively searching for her. The female also actively seeks her young and makes a clucking call. The lost young approaches the female when it hears her call. Merchant and Sharman, 1966, in reporting work on cross-fostering pouch young of different species, stated that macropods of three species - Macropus giganteus, the grey kangaroo; Megaleia rufa, the red kangaroo; and Wallabia bicolor, the swamp wallaby - all have different calls but all responded to the calls of foster young of different species. the authors' implication is that the females learn to respond to the different calls of the young, but again it is the young who do the calling, as opposed to what was observed for W. rufogrisea.

It may be that W. rufogrisea young do call to their mothers if the young are more lost than it was possible to become in their enclosure. The young do return to the pouch spontaneously without being called; perhaps a young might call if it did not readily find its mother upon seeking to return to the pouch. Or it may be, in this species, that it is only the mother who vocalizes when she wants her young to return to her; while the young, if it takes the initiative in returning to the female, does so without calling. It seems more likely that the young do call but that a situation eliciting such calling was not observed. This possibility could be explored experimentally by briefly visually isolating the young from the mother before permanent pouch emergence. This might elicit calling by the young.

Since calling by the female was only observed during the brief transition period when the young comes out of the pouch but is not

permanently out, it would also be interesting to determine if the young responds to the call stimulus only during this period. Recordings of the female call could be played to see if young showed any response to such calls after permanent pouch emergence. Such a response might include attending to the sound and actively searching for the female.

The mother's behavior toward her young changes at permanent pouch emergence with the cessation of calling. Whether or not the young would respond to calling after pouch emergence would hint at the presence or absence of a similar change in the young. If the young no longer responds to a recorded call, its behavior toward its mother - that of responding to her call - has changed as well. If the young still responds, the apparent behavioral change by the young toward its mother - no longer associating with her - is due to a lack of stimulus to which the young responds.

Pouch emergence

An interesting question is who determines the time of final pouch emergence, the young or the mother? As already mentioned, the young seems to fall out of the pouch as the mother relaxes the pouch opening rather than to climb out. Also the mother seems neither to help nor to hinder the young when it re-enters the pouch. If the mother can spill the young out at will but does not prevent its return to the pouch, this behavior does not help to answer the above question.

Sharman and Calaby, 1964, reported for the red kangaroo, Megaleia rufa, that the mother relaxes the pouch opening so that the young falls out, as was observed in W. rufogrisea. However, M. rufa mothers initially aid their young in regaining the pouch when the young first begin to come out, and later prevent the young from re-entering the pouch. In aiding the young, the female bends forward and inclines the hind legs

backward from the normal upright position. This lowers the pouch opening and the young can more easily somersault into the pouch. To prevent the young from re-entering the pouch, the mother puts her forelimbs in front of the young's hindlimbs if it is facing her nursing; otherwise she moves off and avoids the young.

These observations indicate that, for M. rufa, it is the mother who determines when the young shall permanently emerge from the pouch. Nothing was observable to indicate that the same holds for W. rufogrisea, except the mother's relaxing the pouch so that the young falls out. However it is possible that behavior excluding the young from the pouch occurs but was not observed, especially if it does not require a great number of rebuffs to convince a young wallaby that it has permanently emerged from the pouch.

Many macropod marsupials, including W. rufogrisea (Sharman, Calaby, and Poole, 1965), exhibit the phenomenon of delayed implantation: an ovum is fertilized during a post-partum estrus, develops to the blastocyst stage, and lies dormant in the uterus until such a time as it implants and resumes development. This may be after a pouch young has been prematurely lost, or just before the pouch is vacated by a young animal, resulting in birth shortly after the pouch is vacated (within a day for M. rufa, Frith and Calaby, 1969, page 108).

It is possible that the female evicts the young from the pouch in order to accomodate the newborn young which develops from the delayed blastocyst, although there is no evidence supporting this. In fact, Sharman and Calaby, 1964, found in M. rufa that pouch emergence of the young occurred at 235 days post-partum for 16 females which gave birth immediately after emergence of the young as well as for 8 females which did not give birth. The presence of this precise length of pouch life

does seem to indicate that pouch emergence is determined by some physiological factor, probably in the mother, since it seems to be she who insists upon final pouch emergence, at least for M. rufa.

Since the exact ages of the W. rufogrisea young were unknown, I cannot say for how many days the young were in the pouch after birth nor if the three that emerged permanently each spent the same duration of time in the pouch. The females were not checked after the pouch emergence of their young to see if they gave birth immediately following the vaca-tion of the pouch.

Sharman, Calaby, and Poole, (1965) give the length of pouch life for Protemnodon (= Wallabia) rufogrisea as 284 days. They do not state if this is a mean value nor do they say how this figure was obtained. The implication of this is that W. rufogrisea is like M. rufa in having a well-defined, constant length of time that the young spend in the pouch. However since no overt hindrance to the young entering the pouch was observed in our W. rufogrisea, no definite answer to the question of whether the mother or the young determines the time of final pouch emergence is available. One would suspect that it is the mother, however, if what has been observed for M. rufa is at all true for W. rufogrisea.

One incident is relevant here. As mentioned before (page 25), two days before Esther permanently emerged from the pouch, the adult males made repeated sexual approaches to Esther's mother. This may indicate that the mother was coming into a post-partum estrus, if a new young were to be born immediately after Esther's emergence from the pouch.

It is also possible that the mother may terminate the young's pouch life as a non-physiological response to some characteristic of the young such as size or weight. This is only likely if the length of pouch life is variable, since rate of growth would be expected to vary among

individual young.

If enough animals were available, one could explore the two possibilities that pouch life is either a specific length and determined by the physiology of the mother or is determined by the growth rate of the young. If a pouch young which was approaching the point of permanent pouch emergence were removed from the mother's pouch and replaced with a much younger, smaller animal, there are two possible tidy outcomes and one confounded one. If pouch life is a specific length, the younger replacement animal will be evicted at that time which the older original animal would have been - at a specific length of time after the first animal's birth. If the length of pouch life depends on the rate of growth of the young, the foster young will remain in the pouch until it is of a size to emerge.

What may also happen is that the size of the young somehow influences the physiology of the female, and even though pouch life is generally of a specific length, the mother will allow the foster young to complete its pouch life. It is also possible that the female has nothing to do with determining the time of pouch emergence and the young becomes independent when ready, although in view of the work with M. rufa on the female preventing re-entry and the probable specific length of pouch life for W. rufogrisea, this is unlikely.

Ageing the young

Several workers have developed methods of ageing macropod young based on morphological characters such as growth of the hind foot, tail, ear, and weight (Waring et. al., 1955; Sharman and Calaby, 1964; Tyndale-Biscoe, 1968). Taking such measurements requires repeatedly restraining the female and disturbing the young in the pouch. Such treatment is undoubtedly upsetting to both the mother and the young and is thus incompatible

with concurrent behavior studies.

It is possible that some behavioral measures may provide criteria for ageing the young as well. Since the dates of birth for the W. rufogrisea young observed were unknown, only relative ageing of them was possible. Two possible behavioral measures for ageing are the time of permanent pouch emergence and the time of weaning. If W. rufogrisea has a fixed length of pouch life, pouch emergence would be a good means of relative ageing of the young as well as a means of exact ageing after permanent pouch emergence if the length of pouch life is known.

Since the point of complete weaning could not be determined from the data, this measure is not available as an ageing criterion. However each young wallaby showed one major peak in the amount of time spent nursing while out of the pouch; possibly this is of use in ageing the animals. These peaks indicate slightly different relative ages than those obtained from the time of pouch emergence (one to two weeks difference). It may be that, if pouch emergence occurs at a fixed time and is determined by the physiological cycle of the female in some way, the time of pouch emergence fixes a chronological age of the young and the peak in nursing indicates a physiological or maturational age of the young, determined by its rate of growth and the condition of the lactating female, both of which may be influenced by environmental conditions.

Social interactions

In discussing the social behavior of these particular wallabies, it must be borne in mind that this is a confined group of perhaps unnatural size and composition which has been removed from its native habitat. Too little space, too many or too few animals with which to interact, and too many or too few of one or both sexes: any or all of these factors may have affected the observed social behaviors and served to make them

artifacts of the situation rather than valid species patterns. Indeed, subsequent to this study, Heine and three of the adult males died, perhaps due to stress from other animals. (The autopsy reports indicated toxic levels of lead in two of the three males, however.) Heine appeared to have been accidentally suffocated while being sexually assaulted.

During the observation period social interactions were relatively rare occurrences (quantitatively observed for the young and subjectively estimated for the adults). Most of the interactions observed fell into the neutral category. LaFollette's study (1968, 1971) of this group of wallabies showed definite dominance relationships among the wallabies. Individual recognition and deference to a dominant animal will reduce the incidence of open aggression and actual fighting. Even this aggression-reducing social organization may be an artifact of a confined population. As Christian points out (1970), in many animals aggressive behavior increases as crowding increases. For this reason, a captive population of a higher than usual density and no opportunity for dispersal may exhibit types of behavior - aggressive interactions and dominance relationships - never observed in the wild. The confined situation which produces these behaviors may be unnatural, but it does demonstrate that the animal has some capacity to cope behaviorally with unusual population densities and accompanying stresses.

Unfortunately little is known of macropod social behavior in the wild. Frith and Calaby, 1969 (pages 66 -73), report that for M. rufa actual fighting occurs rarely both in the wild and in confined animals. Other sparse information indicates that in the wild macropods form aggregations without social organization; there are no hierarchies or established groups.

BIBLIOGRAPHY

BIBLIOGRAPHY

- Beach, Frank A. (1939). Maternal behavior of the pouchless marsupial Marmosa cinerea. J. Mammal., 20, 315-322.
- Bombardieri, Rocco A., Jr., and Johnson, John I., Jr. (1970). Daily activity schedule of captive opossums. Psychon. Sci., 17(3), 135-136.
- Christian, John J. (1970). Social subordination, population density, and mammalian evolution. Science, 168, 84-90.
- Frith, H.J., and Calaby, J.H. (1969). Kangaroos, C. Hurst and Company, London, 209 pages.
- King, John A. (1955). Social behavior, social organization, and population dynamics in a black-tailed prairiedog town in the Black Hills of South Dakota. Contributions from the Laboratory of Vertebrate Biology No. 67, University of Michigan.
- LaFollette, Robert M. (1968). Dominance relations between Bennett's wallabies, Wallabia rufogrisea frutica, confined to a yard. MSc. Thesis, Michigan State University.
- LaFollette, Robert M. (1971). Agonistic behavior and dominance in confined wallabies (Wallabia rufogrisea frutica). Anim. Behav., in press.
- Mackerras, M.J., and Smith, R.H. (1960). Breeding of the short-nosed marsupial bandicoot, Isoodon macrourus (Gould) in captivity. Aust. J. Zool., 8, 371-383.
- Marlow, B.J. (1961). Reproductive behavior of the marsupial mouse, Antechinus flavipes (Waterhouse) (Marsupialia) and the development of the pouch young. Aust. J. Zool., 9, 203-218.
- Merchant, J.C., and Sharman, G.B. (1966). Observations on the attachment of marsupial pouch young to the teats and on the rearing of pouch young by foster mothers of the same or different species. Aust. J. Zool., 14, 593-609.
- Rood, J.P. (1970). Ecology and social behavior of the desert cavy (Microcavia australis). Amer. Midl. Natur., 83(2), 415-454.
- Sharman, G.B., and Calaby, J.H. (1964). Reproductive behaviour in the red kangaroo, Megaleia rufa, in captivity. CSIRO Wildl. Res., 9, 58-85.

- Sharman, G.B., Calaby, J.H., and Poole, W.E. (1965). Patterns of reproduction in female diprotodont marsupials. J. Reprod. Fert., 9, 375-376.
- Tyndale-Biscoe, C.H. (1968). Reproduction and post-natal development in the marsupial Bettongia lesuer: (Quoy and Gaimard). Aust. J. Zool., 16, 577-602.
- Waring, H., Sharman, G.B., Lovat, D., and Kahan, M. (1955). Studies on marsupial reproduction I. General features and techniques. Aust. J. Zool., 3, 34-43.

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