1991

Development of motor skills in the California sea otter pup (Enhydra lutris)

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Order Number 1344257

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San Jose State University, 1991

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DEVELOPMENT OF MOTOR SKILLS IN THE CALIFORNIA SEA OTTER PUP (*ENHYDRA LUTRIS*)

A Thesis

Presented to

The Faculty of the Department of Biological Sciences

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

By

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May, 1991

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Acknowledgements

It seems incredible that after so many years of gathering, analyzing, and worrying about these data, it has finally come time to thank in print all those who have helped.

The biologists and biostatisticians at the California Department of Fish and Game deserve the most heartfelt thanks. Jack Ames took me on as an intern in 1979, then kept me variously employed for several years while I gathered and processed data. His years of experience with otters, his candid eye, and his sincere doubt that I could ever finish this work did the most for making sure I did. John Geibel wrote the dBASE II program that did the original data processing, without which nothing would have progressed. Phil Law provided further data reduction. Ron Jameson and Jim Bodkin of the U.S. Fish and Wildlife Service offered their time, access to information on local tagged otters, housing, and good cheer whenever I worked at the Piedras Blancas station. Dave Schwartz helped with field observations long enough to allow me a brief vacation. Marianne Riedman offered editorial comments and access to unpublished data. Thesis committee members Jim Harvey, Jim Estes, Mike Foster, and Bob Brownell are gratefully acknowledged for their encouragement and editing of this work. Bernd Wursig served as thesis advisor, offered access to his laboratory and personal equipment, and presented many insights on both ethology and data analysis. Use of the Questar telescope was provided by Moss Landing Marine Laboratories. Partial funding was provided by a Packard Foundation Grant and a Sigma Xi Grant-in-Aid-of-Research.

Family and friends at home provided on-going support. My husband Dan offered unquestioning understanding and a relaxing place to write, and became at the end the sole wage-earner while I finished. Barbara Luther, Margaret Faurot, and Jean Daniels are heartily thanked for providing the care for my children that gave me the freedom to work. The curiosity and laughter of my young son Ian and my infant daughter Cayley kept me reminded of why the process of behavioral development fascinates, and why the "why's" need to keep being answered.

ABSTRACT

DEVELOPMENT OF MOTOR SKILLS IN THE CALIFORNIA SEA OTTER PUP (ENHYDRA LUTRIS)

by Ellen R. Faurot-Daniels

Sea otters (Enhydra lutris) are excellent research subjects from the perspectives of evolution, natural selection, ecology, behavioral biology, and resource management. They are easily observed, and most behaviors (including pup-tending) are performed at the water's surface, allowing nearly complete collection of behavioral information.

Ten California sea otter pups of known age were observed periodically from birth until separation from their mothers. Sixty-one behavioral categories were recorded; 22 behaviors were specific to development of pup motor skills. Percentage of active period, frequency rate, and mean duration of each behavior were compared with pup age.

Two pups developed motor skills at rates very different from the others. All pups showed a high degree of individual variability, indicating that behavior alone cannot be used to determine chronological age of pups. Varying learning rates and patterns can be assessed and may be applicable to evaluations of future reproductive success.

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Introduction

Sea otters (*Enhydra lutris*) are excellent research subjects from the perspectives of evolution, natural selection, ecology, behavioral biology, and resource management. Surface activities of undisturbed wild otters can be viewed easily with high-power telescopes from many points along the central California shore, and their subtidal foraging zones are usually within SCUBA range of community and subtidal ecologists. Equipment needed for data collection and analysis can be quite simple and inexpensive, making sea otters ideal study animals for logistic and economic reasons as well.

All marine mammals must deal with the selective pressures of living at sea, but sea otters, the most recent mammal to resume an obligate dependence on the ocean (Estes 1989), have fewer physical and physiological advantages. Lacking the thick blubber layer used by cetaceans and pinnipeds for warmth, buoyancy, and food storage (Daugherty 1979), the sea otter must rely instead on thick fur, persistent cleaning and aeration of the fur, and a high metabolic rate to meet its similar needs (Kenyon 1969, Estes 1980, Costa et al. 1982, Costa et al. 1984). Evolutionary advancement in cetacean and pinniped respiratory and circulatory systems gives them the ability to make deep dives in pursuit of prey (Irving 1966, Kanwisher and Sundnes 1966, Lang 1966, Le Boeuf et al. 1986), and streamlined forms and powerful muscular systems can propel them far from shore for extended periods. Sea otters have not reached similar levels of adaptation, and as a result are tied to food resources that generally occur within 1 km of shore and in waters < 40 m (Estes 1980). Essentially all food handling, grooming, care of young, and social interactions occur at the water's surface. It is these very limitations that make sea otters the most easily and completely observable marine mammal.

Sea otters also are intriquing subjects for comparative studies with other members of their order (Carnivora), family (Mustelidae), and subfamily (Lutrinae). Their polygynous mating system and solitary (sensu Sandell 1989, p. 164) lifestyle are more akin to bears and cats (Klieman and Eisenberg 1973) than to the harems of pinnipeds, or the extended and cooperative "families" of many cetaceans. They are the only member of the Mustelidae to turn so completely to a marine existence--their weasel, badger, skunk and river otter relatives occasionally and variously use fresh and marine waters for foraging or travel, but are tied to land for reproduction. Sea otters and river otters have similar morphologies, activity patterns, food preferences, and "plastic" breeding seasonalities (Melquist and Hornocker 1983, Estes 1989), but differ markedly in the ways they birth and care for their young. River otters sequester their 2 to 5 altricial young in dens for up to six weeks following parturition (Nowak and Paradiso 1983). Sea otters generally bear only one precocial pup at a time (but see Jameson and Bodkin 1986); mother and pup are usually highly visible at the water's surface for the entire pup-dependency period. Research on known-age sea otters therefore can answer many questions on development of motor and social skills, life history parameters, and future reproductive success that cannot easily be addressed by studies on denning carnivores or mustelids.

Sea otters have been the focus of community ecology studies for 15 years (Estes and Palmisano 1974, Cooper et al. 1977, Estes et al. 1978, Simenstad et al. 1978, Duggins 1980, Lowry and Pearse 1974, Hines and Pearse 1982). Because of their high metabolic rate, they consume the equivalent of 15 to 35 percent of their body weight daily (Costa 1982). Preferred invertebrate prey (abalone, sea urchins, clams, crabs) are taken from soft or rocky shallow subtidal and intertidal areas (Ebert 1968, Vandevere 1969, Miller et al. 1975, Stephenson 1977).

After these prey are depleted, the diet broadens to include mussels, turban snails, squid, octopus, chitons, tubeworms, barnacles, scallops, and sea stars (Wild and Ames 1974). Sea otters can greatly influence the abundance and distribution of prey populations, and concomitantly, the community ecology of the giant kelp beds in which many of their prey occur. They are considered by many to fit Paine's (1969) concept of an ecological "keystone" species, although this issue has been a subject of debate (Cowen et al. 1982, Foster and Schiel 1988). Regardless of the final settlement of this question, no one familiar with nearshore ecology denies the profound effect sea otter predation can have on invertebrate populations. Information gathered on sea otter biology and behavior will continue to be very important in studies of kelp forest and soft bottom community ecology.

Extensive commercial exploitation for their fur brought sea otters to the brink of extinction by the early 1900s. Although now protected by international treaties and federal and state legislation (Miller 1974), sea otters are at the center of human/otter conflict over commercial crab, sea abalone, sea urchin, and set gill-net fisheries (Miller 1974, Wild and Ames 1974, Wendell et al. 1986). Debate over future oil exploration and development along the central California coast pivots around sea otters. Continued gathering of scientific data on sea otters therefore is of intense interest to parties on both sides of fisheries-management and oil-development issues.

Data on behavioral development of sea otters is necessary in each context discussed above. Without a full understanding of how behaviors develop, we could only guess at the adaptive significance of ontogenetic patterns and their relation to the immediate situations of the young animal and its later reproductive activities and fitness (Bekoff 1989).

Although quantitative data are available on time budgets (Shimek and Monk 1977, Loughlin 1978, Estes et al. 1986, Garshelis et al. 1986) and home ranges and territoriality (Loughlin 1980) of adult sea otters, quantitative information on pups has generally been lacking. Sandegren et al. (1973) were the first to make systematic, quantitative observations of sea otter mother-pup relationships, but their observations did not involve longitudinal tracking of known-age pups. In 1981, an ethogram (a description of the behavioral repertoire, the first step in any behavioral study) was developed for adult sea otters (Packard and Ribic 1981). Payne and Jameson (1984) watched 15 mother-pup pairs, 13 of which included tagged mothers. They worked with known-age pups, but did not gather extensive quantitative data; most of their information was from one pup. The acquistion, refinement, and application of each skill by sea otter pups was not quantitatively described.

In addition to providing quantitative baseline data on behavioral development, this study attempted to determine if the age of wild pups could be estimated from behavior alone. If acquisition and performance of motor skills followed a predictable pace and pattern, then a developmental timeline, based on known-age pups, could be constructed. A minimal data set of behavioral observations on an unfamiliar pup would allow comparison against the timeline and assignment of a birthdate. More pups could then be included in studies of age- and sex-related mortality and other life history parameters.

This study focused on ten known-age pups of tagged California sea otter mothers. Pups were watched from birth until they were separated from the mother by either death or weaning. Quantitative data on the development of 22 behaviors are provided and their refinement over time discussed. It is anticipated that these results, coupled with those from a companion study on development of social interactions and skills (Faurot-Daniels in prep.), will lead to greater understanding of the pattern of development in the sea otter, and hence its natural and life histories. Information from this study can be applied to broader questions of comparative biology, ecology, and resource management.

Methods

Field observations

Observations of mother-pup pairs were made from two coastal sites along central California. Seven mothers and eight pups (one mother with two successive pups) were observed from the Monterey harbor breakwater (121°54'W, 36°37'N) to Point Pinos (121°55'W, 36°35'N). The remaining mother and her two successive pups were observed in kelp beds near Piedras Blancas (121°16'W, 35°40'N). Field observations were made from 9 April 1981 to 28 December 1983. Data were collected during 630 h of observations; 135.2 h of behavioral ontogeny data were recorded on tape, and 100.4 h of useful data were used in analyses.

Mother otters of each pair were flipper-tagged before the beginning of this study by the California Department of Fish and Game (CDFG) (Ames et al. 1986) and by the U.S. Fish and Wildlife Service (USFWS). This allowed individual recognition of each tagged otter. Tags of nearshore otters could be seen from shore by observers using high-resolution binoculars or telescopes.

Groups were scanned frequently before collection of behavioral data to determine the nature and composition of the otter population in the Monterey Peninsula area. (Appendix 1 lists the classes of information recorded for each otter during scans). Although it was often difficult to resight particular tagged otters of interest from one day to the next, most were seen at least once a week. Observations of the seven Monterey Peninsula females were frequent enough to estimate birthdates of their newborn pups to within a few days (Table 1). Similar closely spaced scans by USFWS biologists working near Piedras Blancas allowed a tagged female otter from that area with two successive known-age pups to be included in this study.

All otters in the study area were scanned until one of the tagged mothers with a known-age pup was spotted. The scan was then abandoned while behavioral activities for the pair of interest were recorded on tape. Taped observations of the pair continued until the pair was lost from view (due to movement, poor viewing conditions, or the onset of darkness) or if they ceased activity and began a prolonged resting bout.

All observations were made from shore, and most were made using a Questar 50x-80x telescope. Otters occurring within 30 m of shore were viewed with binoculars or the naked eye.

Sixty-one categories of motor and social behaviors were scored, allowing description of actions and interactions of mother, pup, and otters interacting with mother and/or pup (Table 2). Twenty-two categories were specific to pup motor skills (defined in Table 3). Mother and pup were treated as simultaneous focal animals; behaviors were observed and recorded for both unless mother and pup were so separated that only one could be under continuous observation. In these cases, only pup data were recorded. If two mothers with known-age pups were in the same area at the same time, observations were attempted for both pairs.

Behaviors for both mother and pup were timed to the nearest second as the pair was observed through the telescope. A new time mark and behavior would be called into a hand-held tape recorder with each change in behavior by either mother or pup. If one pair member changed behavior but the other member of the pair was still engaged in its previous behavior, then the record for the second member continued as before. A complete "bout" of behavior ran from its initial time mark until the beginning of the next new behavior (onset of a new behavior signaled an ending to the previous behavior); elapsed time was derived later by computer. Certain actions were not mutually exclusive, but occurred simultaneously (e.g., grooming by stroking/rubbing/ rolling, grooming while traveling, feeding while traveling, periscoping while stroking). Behaviors occurring in combination were noted as such on the tape and checksheet (discussed below), but treated separately in analysis. Any observations not fitting pre-described categories were included in the daily field journal.

Data analysis

Taped observations were transcribed onto a checksheet, with behavior, onset time, and initiating pair member clearly noted. Clock times missing from the original tape recording were included on the checksheet by timing directly from the tape. A journal of transcription notes (observations not applicable to the checksheet or included in the field journal) was made simultaneous with the tape transcription process.

Checksheet entries were entered into a dBASE II computer database and durations (seconds) of each bout of each behavior were calculated. Behavior durations and their onset times were recorded to a second database that contained mother identification number, pup age (days), and date the pair was observed.

Data were pooled by age (Table 4). Two-week intervals (represented in tables as age intervals 1 to 7) were used until a pup age of 14 weeks. This allowed reasonable data reduction without losing necessary detail, and bracketed the one- to ten-day uncertainty period around the assignment of each pup's birthdate. Mother-pup pairs often became difficult to locate and follow after the fourteenth week, and there is a reduction in the amount of data collected during those weeks that reflects that difficulty. To make "percentage of total minutes" (Table 4) roughly comparable for older pups, the observations for age intervals 8 (representing weeks 15 to 20) and 9 (representing weeks 21 to 26) were pooled.

Though ten pups were included in the study, most observations came from 5 pups (Table 5). Due to the small sample size, data from all pups were pooled. However, effects on data by particular individuals are discussed where appropriate.

To chart changes in pup behavioral development, it was important to focus observations and analysis on periods when the pup was most active. "Resting quiet" periods were eliminated from data analysis; all calculations and graphs were based on "active" periods only. Proportions of inactive (resting quiet) periods to active (all other behaviors) periods are shown in Table 6.

The following measures were computed for each age interval period:

1. Percentage of active period (hearafter "percent")

   Percent = (Totbeh/(TotObs-RestQu-Outsgt)) x 100

   TotBeh = Total seconds during age interval spent in a given behavior
   TotObs = Total seconds in observation periods within age interval
   RestQu = Total seconds during age interval spent resting quiet
   Outsgt = Total seconds in age interval spent out of view of observer (does not include diving)

2. Frequency rate

   Freq. rate = (NumBeh/(TotObs-RestQu-Outsgt)) x 1000

   NumBeh = Number of times during age interval a given behavior was initiated
   TotObs = As above
   RestQu = As above
   Outsgt = As above

   Frequency rate includes a multiplier of 1000 to facilitate graphing.

3. Mean, standard deviation

   Some means calculated by computer using statistical software (SAS); most means and all standard deviations taken from hand calculator. "Complete" refers to bouts with good "start" and "stop" times.

   Mean = TotCom/NumCom

   TotCom = Total seconds spent in complete bouts of given behavior
   NumCom = Number of complete bouts of given behavior

Each lateral roll, shoulder roll, and forward roll was subjectively classed as "complete" or "incomplete" depending on the proficiency with which the pup performed it.

Diving was classified as foraging or non-foraging. Non-foraging dives were used in travel or play, where shallow porpoising through the water or kelp beds was common. A dive also was considered non-foraging if it was used to retrieve a non-foraging item (the item could not be used as food or tool). Foraging dives resulted in the procurement of food or an appropriate tool (e.g., rock or shell). A series of unsuccessful dives were considered foraging-related if they ultimately resulted in gaining food or tool.

Manipulation of food items was divided into manipulation with consumption, and manipulation without consumption (manipulation of non-food or non-tool items was classified as environmental exploration).

A chest-pounding event was considered "complete" if it included both an appropriate food item and an appropriate tool. The tool could be on the chest, with food pounded against it (e.g., clam against rock), or in some cases food was on the chest and another food item pounded against it (e.g., clam against clam). Occasionally, the food was on the chest, with a small tool pounded against it (e.g., small rock against clam). An "incomplete" chest-pound was defined as involving inappropriate items or combinations (e.g., food pounded against bare chest, rock on chest but pounding without food in paws, food pounded against kelp, two rocks pounded against each other).

Equal amounts of data for each pup for each age interval could not be gathered. Constraints on data collection arose because wild otters and the elements could not be scheduled. Sampling, therefore, was opportunistic rather than random. Samples also were not independent (the same pups were used throughout the study). Statistical analyses could not be made.

Results

Only graphical analysis of results is given. The values for each bar, the sample size (n) used in each calculation, and the standard deviation associated with each mean are given in the tables of Appendices 2 and 3.

Percentage time resting alert (Fig. 1) decreased as pup age increased. Frequency rate, with the exception of a modest peak at weeks 3-4, did not appear to change as pups aged. Mean bout length (duration) showed a general decrease with increasing pup age. The peak at weeks 13-14 was due to one long bout of resting alert by the 89-day-old pup of Red 51; both mother and pup had just awakened, but continued to rest with eyes open before beginning a grooming session.

No pups were observed grooming by rubbing during their first two weeks of life (Fig. 2). After week 3, percentage time spent in this behavior exhibited a modest increase. Frequency rate increased dramatically. The average rubbing session lasted from 25 to 70 sec, but did rise or fall markedly over the 26 weeks. Increased percentage of time rubbing is reflective of increased frequencies as pups aged, not of increased bout durations.

There were also no bouts of grooming by stroking observed for weeks 1-2 (Fig. 3), but after week 3 the pattern was very similar to that for grooming by rubbing, with which it often occurred simultaneously. Again, because mean bout durations remained relatively steady, it was the dramatic increase in frequency rate over time that was responsible for the rise in percentage time spent grooming by rubbing.

Percentage time grooming by licking (Fig. 4) showed a peak at weeks 13-14 that was attributed to the 89-day-old pup of Red 51. The pup engaged in two long bouts of licking; the first bout was part of vigorous grooming coupled with stroking, the second involved only licking. The second bout came at the end of the grooming session, and duration stretched as the pup shifted to a brief period of resting alert. Eliminating these two licking bouts would make grooming by licking comparable for all age intervals. The rise in frequency rate at weeks 11-12 was due largely to the pup of Red 51 at age 80 days. The pup performed 21 of the 37 bouts recorded for this age interval, with 15 bouts part of one grooming session. Mean bout length showed a peak at weeks 1-2 and weeks 13-14. The first peak was entirely attributable to the 9-day-old pup of Red 43, who engaged all three bouts of licking recorded for this age interval. The second peak reflected the case discussed above with the pup of Red 51 and percentage time.

Pups began trying to roll as part of grooming by week 3. Rolls occurred quickly, and execution of a series of them did not usually take long. This is apparent in the graphs. Combined incomplete and complete lateral rolls (Fig. 5) never comprised more than 3% of the active period. Frequency rate, especially of complete rolls, increased after week 8. Combined incomplete and complete shoulder rolls (Fig. 6) in weeks 13-14 accounted for over 11% of the active period, but for all other pup ages the value was considerably lower. Frequency rate showed the same general rise, especially of complete rolls, seen with lateral rolls. Mean duration of shoulder rolls was high in weeks 13-14 due to one long, lazily executed incomplete shoulder roll by the pup of Red 51 at 89 days. Eliminating that roll from the data makes mean duration comparable across all age intervals. Data for forward rolls are available (Appendices 2 and 3), but their low overall frequency did not justify a separate graph.

Grooming by hanging made up nearly 3% of the active period for weeks 5-6. Twenty of 25 bouts recorded for this interval were performed by the 29-day-old pup of Red 64. The hanging was actually not grooming related, but occurred as part of the pup's dive attempts (discussed below) or from looking into the water as the mother dove. For all other intervals, percent hanging amounted to less than 0.25%; data were not sufficient to graph.

Grooming by bubbling occurred at such a low percentage to be scarcely apparent on the graph (Fig. 7), but percentage (Appendix 3) and frequency rate both increased with increasing pup age. Mean durations were generally 30 sec or less, although the first pup of Light Green 398 had a 100-sec session of bubbling while traveling during weeks 7-8.

The data for grooming by headshake, a behavior scored for frequency only, appears in Appendix 3 but was not graphed. The data indicated no trend with changing pup age.

Percentage time spent grooming mother (Fig. 8) was greatest for weeks 1-6; frequency rate also was relatively high during this period, as it was for weeks 21-26. Mean durations were less than 40 sec, with an exception in weeks 3-4 of one 124 sec bout by the 17-day-old pup of Red 64.

Travel with the dorsal surface down (dorsal travel) (Fig. 9) was low for the first 10 weeks, then increased after week 11. Frequency rate increased after week 9 as older pups became more proficient at dorsal travel and began switching more often between ventral and dorsal travel modes. Dorsal travel never was used for more than 40 sec at a time. At weeks 21-26, dorsal travel dominated ventral travel.

Ventral travel (ventral side down) was used since birth (Fig. 10), and was the travel mode of choice when pups became more mobile after week 4. Though pups began using dorsal travel more steadily after week 9, frequency rate for ventral travel remained high. Ventral travel durations, like those for dorsal travel, never exceeded 40 sec.

Pups suckled (or were in the suckling position) during 15-45% of the active period; percentage time spent suckling was greatest during the 21-26 week age interval (Fig. 11). A high frequency rate for weeks 21-26 indicated that pups often were successful in their suckling attempts. However, journal and tape transcription entries noted that the mother often tried to shun the pup when it got older, or broke off nursing before the pup was finished. Data for mean duration indicated that younger pups were able to suckle unhindered for longer periods.

Periscoping (Fig. 12) was a quickly-occurring behavior scored for frequency only. Adult otters took this position when scanning the area, and it was commonly seen preceding a dive. Most pups did not begin diving until weeks 7-10, so periscoping also was generally absent in the early weeks. It was first recorded for these pups at week 7, and then showed a modest increase with age. Older pups were more proficient at this behavior, capable of assuming and maintaining a vertical posture in the water for extended periods. A "good" periscope often led into a high, arcing dive, also more commonly seen with older pups.

The earliest dives were recorded for the 29-day-old pup of Red 64 (Fig. 13). This pup was very active from an early age, and played often and energetically with the mother and objects in the environment. At day 17, the mother repeatedly rolled onto her stomach, holding the pup in her teeth. The pup's face would be submerged for up to 50 seconds, equivalent to the average duration of an adult dive (Estes 1980). The mother would roll back onto her back from time to time to allow the pup to breathe. This action subdued the pup, and may have functioned as early breath-holding exercises. At day 21, the pup bit and lunged at the mother's face, but the mother did not submerge the pup. By day 29, the pup would swim ventrally at the water surface, looking into the water during several of the mother's dives. Early on day 29, the pup submerged on its own if held underwater by a patch of kelp. In open water later that day, the pup could, with several strong kicks, get and stay below the surface for several seconds at a time. Twelve dive attempts were recorded for this pup on day 29. This was the only pup observed diving with its buoyant natal pelage. It also was seen diving on days 37, 45, 52, and 57. The first pup of Dark Green 1453 made one dive attempt on day 43, but otherwise, no other otter pups were seen diving until day 64. By this time, the adult pelage was in place. All pups, with the exception of Red 43's, were diving by day 83 (the pup of Red 43 was never seen to dive). Dives averaged 30 to 45 sec, depending on pup age, but often exceeded 60 sec.

Pups began exploring food items in weeks 1-4 (Fig. 14), but did not begin eating them until week 5. Even after week 5, pups often would handle a food item without eating it. Younger pups seemed unable to break into and consume hard-shelled food; for older pups, non-consumption often apparently was a result of satiation. Chest-pounding attempts began at weeks 5-6 (Fig. 15) for the pup of Red 64, the same age at which it began diving. Chest-pounding did not begin earlier, even though pups were handling food in weeks 1-4. Cases of complete chest-pounding in early weeks (5-8) seemed almost accidental.

Mothers were fairly consistent in giving food to pups after pups began showing interest in solid food after week 5. Pups became very persistent in taking food after week 7. Pups could be quite forceful; food not offered would often be grabbed from the mother's paws or mouth.

Percentage time and frequency rate of environmental exploration were generally steady for weeks 5-12 (Fig. 17), after which they declined as pups became increasingly more involved in their own grooming, diving, feeding, traveling, and interactions with others.

Although otters make a variety of sounds (Packard and

Ribic 1981), only screams could be heard clearly from shore. Screams occurred mostly as a result of separation, and most separations were due to diving. Young and apparently curious pups would often travel quite a distance on the water's surface during a mother's dive, and even a resting pup could drift away. After surfacing, a mother separated from her young pup would scream until the returned screams of her pup would guide her back to it. Confusion was increased as pups began independent diving, and frequency rate of pup vocalizations climbed accordingly (Fig. 18). After weeks 7-8, pups appeared more responsible than mothers for maintaining visual contact. A mother surfacing from a dive would often deliberately evade the pup long enough to eat some of her food; her relative silence and distance from the pup probably contributed to an increased frequency rate of pup screaming in later age intervals.

Discussion

Ontogeny of motor skills: Findings from this study.

Two pups seemed exceptional for different reasons. The pup of Red 64 first attempted independent dives when it was only 29 days old; this was about a month before most pups began losing their woolly and buoyant natal pelage, allowing them to dive. In contrast, the pup of

Red 43 was never seen making an independent dive during the 248 days it was observed with the mother. These two pups comprised 20 percent of the study sample. If this small sample represented the population, then there were strong differences between individuals in rates of development. This also indicated that behavior alone could not be used to determine the age of an unfamiliar, wild pup.

Mean durations and associated standard deviations (Appendix 3) also indicated differential performances by each individual. Standard deviations equaled or exceeded means for almost every behavior, indicating that pups do not execute behaviors the same way from one bout to the next. Very general trends in sea otter behavioral development can be discussed only if awareness of marked individual differences is maintained.

Discussion of behaviors

Resting alert is not a "skill" that needs to be developed. Like resting quiet, it is a state of being manifested in its complete form from birth. It does, however, seem to change with age. After week 4, time formerly spent in extended bouts of resting alert was used instead for grooming, traveling, and feeding. Resting alert continued to occur, but in shorter, more frequent bouts.

Grooming by rubbing the hind feet together was a motor skill that improved with age. Rubbing was very rudimentary for the first 4 to 8 weeks; pups often were seen making the motion, but not connecting the feet. By about nine weeks, most pups were capable of complete and proficient rubbing. At nine weeks, most pups also were able to simultaneously perform rubbing with one or more other behaviors (licking, stroking, rolling, bubbling, traveling). The pup of Red 64, apparently not involved in developing diving skills, was more capably performing sets of grooming behaviors at age 5-6 weeks.

Stroking and rubbing developed at the same rate. They did not occur in any particular order, but almost always occurred together. Rubbing and stroking appear in combination more than other grooming behaviors, and can probably be considered a developmental unit.

Licking was steadily performed from birth. Unlike rubbing and stroking, which appear rudimentary at first but then steadily developed, the efficacy of licking cannot be determined by the shore observer. It is likely that it too is conducted with greater efficiency as pups age, but this cannot be determined from behavioral observation alone.

The complex techniques involved in lateral, shoulder, and forward rolling required practice. Incomplete rolls were replaced more consistently with complete rolls as pup age increased, but 26-week-old pups were still performing many incomplete rolls. Rolling skills probably continue to develop even after the pup separates from the mother.

Bubbling by otters may function to aerate the fur, or the bubbles may be the result of underwater expirations. If it functions as an aeration technique, its efficacy cannot be judged by an observer. Although the posture for bubbling occurs with greater frequency with increasing pup age, observational constraints make functional interpretation difficult; this behavior cannot yet be evaluated in terms of behavioral development.

Pup grooming mother showed two peaks, the first in weeks 1-6, the second in weeks 21-26. Occurrence in the first six weeks may be part of bonding with the mother; in weeks 21-26, it may signal a shifting of the responsibility for maintaining the mother-pup bond from the mother to the pup.

Sea otter pups were capable of ventral travel from birth, but had to learn the skills of dorsal travel. Pups continued to favor ventral travel even after the acquisition of dorsal travel skills at about week 10. Directional use of visual, olfactory, and auditory senses are probably facilitated by ventral travel.

Pups suckled during the entire pup-dependency period. Weaning occurred at the time of final separation from the mother. Older pups attempted suckling at almost every opportunity, but were often shunned by their mothers. Journal notes indicated that pups were least successful at suckling when the mother was feeding. Some pups may not have been proficient enough at diving and food manipulation to meet their own energy needs, while other pups were able to procure their own food but still received most of their prey from their mother's captures (Marianne Riedman, pers. comm.). Dual demands for milk and prey may have placed a great strain on the mother. Emaciated mothers of older pups were seen feeding on California mussels and gooseneck barnacles from wash or shoreline rocks. Though the mussels were valuable calorically, the barnacles were not (Faurot et al. 1986). Mothers of pups at the very demanding 3- to 6-month ages were seen on three occasions foraging within high wave-energy zones that could be very dangerous to inexperienced animals. Single females specializing in mussels and barnacles, and females in estrus, have also been reported using this resource (Marianne Riedman, pers. comm.).

All foraging-related skills required long periods of practice. Periscopes were not evident until the pups began making independent dives. The periscopes of pups at 7 to 14 weeks were typically brief and low-profile. The very pronounced periscopes (high profile, rigid posture, scanning function) of adults were regularly manifested by 15- to 26-week-old pups.

Foraging dives were a large component of total dives once pups acquired this skill. Not all foraging dives, however, were successful. Pups 5 to 10 weeks old were unsuccessful on most dives; pups became more adept after 10 weeks, and successfully surfaced with at least a small food item from almost all dives by 15 weeks.

A high proportion of incomplete versus complete chest-pounds throughout all age intervals indicated that this behavior required much practice. There is some indication from observations of captive pups (Faurot-Daniels, pers. obs.) that this is a socially-facilitated behavior. Otters in isolation exhibit a great deal of general pounding behavior, but it is problemantical whether complete chest-pounding (using appropriate tool, food, and action) would develop in the absence of a skilled role model.

As discussed above, mothers of older (3+ month) pups often were greatly stressed in providing enough food to meet their own metabolic needs as well as those of their growing pups. Mothers continued to give food to pups throughout the entire dependency period, but often not before trying to evade an older pup. A foraging mother could evade her pup by surfacing well away from her pup, by swimming away once she was on the surface, or by turning her head from the pup or snapping at it when the pup reached for food. Mothers of older, aggressive pups were especially forceful if the pup reached for food before the mother had eaten.

Environmental exploration was at its greatest level for 5- to 12-week-old pups. Pups in this age group are active and curious. With an involvement in diving and the handling of food and tools came a concomitant increase in the handling of other items found in their environment. Sticks, kelp fronds, marker buoys, and litter were common items of exploration and play. Most bouts of environmental exploration occurred while a pup waited on the surface for its mother to finish a dive.

Mothers responded to pup screams less as pups aged. Changing size of the pup vocal apparatus may have changed the pitch of vocalizations, and allowed changes in behavioral patterns as well. As pups aged and become more demanding and more independent, mothers used the pup's screams to visually relocate them, but did not approach them for retrieving.

Ontogeny of motor skills: Findings from other studies

An earlier study (Payne and Jameson 1984) provided support for some of the observations noted here. Although no quantitative data were reported, the one pup they watched for extended periods behaved in a manner very similar to that reported for eight of the ten pups of this study. Payne and Jameson noted a transition from passive resting to active swimming at age 4-5 weeks, the first successful dives at age 6 weeks, ingestion of solid food at 6 weeks (corresponding to first independent dives), and the first complete case of tool use at age 19.5 weeks. Grooming was rudimentary in early weeks, but well developed by age 14 weeks. The transition from ventral to dorsal swimming occurred by week 10.

On-going studies of wild Monterey otters have been conducted by Monterey Bay Aquarium researchers and are currently being summarized. Field observations focused primarily on foraging mother-pup pairs. Preliminary results show marked individual variation in pups in acquisition and performance of skills and in mother-pup interactions.

Individually distinctive foraging strategies apparently are transferred from mother to pup, and may persist in the pup's repertoire after weaning (Riedman et al. 1989). Pups in general were much less successful than their mothers in acquiring prey. Approximate values for mean percent foraging success are as follows (Riedman et al. 1990):

Pups (all ages combined)	Mothers
77% Unsuccessful dives	30% Unsuccessful dives
13% Dives result in prey	70% Dives result in prey
10% Dives result in non-prey	0.1% Dives result in non-prey

These averages do not reflect the large individual variation present.

Pronounced individual variation was also observed in foraging-related interactions of different mother-pup pairs (Riedman pers. comm.). Termination of pup suckling was more abrupt with some mothers than with others; in some cases, even inactive mothers would push away older pups attempting to suckle. Incidences of mother giving food or pup taking food evidenced varying levels of aggression depending on the pair observed. Some mothers were seen giving their tools and their food to pups, while other mothers evaded pups and denied their solicitations for food.

Limitations of this study and recommendations for future work

Only a portion of the adult sea otter behavioral ethogram described by Packard and Ribic (1981) was used in this study. The small sample size of this study (most data collected from 5 pups), the possible effects of successive pups of mothers, and the lack of independence in sampling, are all confounding effects to be considered in analyses and interpretations of these findings.

Data were collected for both mother and pup, but behaviors assigned to the mother were not given the same detail given to pups (for instance, pup grooming was subdivided into nine separate behaviors, whereas mother grooming self was not similarly divided). Data on mother-pup interactions and interactions with other otters were collected at the same time as the motor skills data but will be analyzed separately. Data for the mother were, and should continue to be, collected for studies of mother-pup interactions, but should be included in studies of pup motor skill developoment only when they directly relate to the pup (e.g., food sharing, vocalizations). As it is still not clear which behaviors prove most interesting by future studies, it is recommended that each behavioral category used here continue to be included.

Data analysis could be simplified by considering more behaviors for frequency only. It is suggested that behavior be treated as follows:

Timed behaviors	Frequency-only behaviors
Resting alert	Grooming by hanging/bubbling
Grooming by rubbing	Forward roll
Grooming by stroking	Shoulder roll
Grooming by licking	Lateral roll
Groom mother	Periscope
Play with mother	Mother gives food to pup
Nurse	Pup takes food from mother
Dive	Mother vocalize
Manipulate food	Pup vocalize
Chest pound	
Travel dorsal	
Travel ventral	
Environmental exploration	

It also is recommended that the several behaviors described in the ethogram of Packard and Ribic and listed below be included in future ontogenetic studies:

Motor skills	Social skills
Rock	Bite
Folding dive	Chase
Row	Clasp
Side-stroke	Grab
Dunk	Tumble
	Wrestle

There were distinct advantages and disadvantages to the sampling and analysis methods used in this study; some are reflective of otter behavior, and some are simply reflective of the difficulties in studying otter behavior.

The continuous sampling technique used in this study provides a wealth of detailed and sometimes superfluous information that is difficult to analyze. The detail was useful in this case because it caught quickly or rarely occurring behaviors. Continuous sampling also allowed calculation of means and standard deviations, and the wide standard deviations around nearly every mean indicated that the otter pups were much more variable than expected. This provided an objective line of evidence for the subjective impressions developed during the field observations.

Basing calculations on just the active period was a method adopted when it was discovered that otters could not be sampled according to a convenient schedule. It seems a good way to restrict the data to just that needed for analysis of behavioral development. Otters would need to be under 24-hour watch only if activity budget information were desired.

Difficulties of ontogenetic study

It is often very difficult in behavioral research to choose behaviors most appropriate for answering a specific research question. Chalmers (1980) noted that dividing an animal's behavior into a number of functionally defined categories, and examining each in isolation from others, may keep a researcher from getting a good picture of overall development. If several behaviors rely on common underlying postural, manipulatory, or locomotor skills, none of the behaviors may develop until the underlying abilities appear. Many distinct sea otter behaviors, variously associated with resting, grooming, traveling, feeding, or interacting with others, will often occur in more than one context. Rolling, for example, is commonly noted as grooming behavior, but grooming by rolling may occur on its own, as part of traveling, or as part of feeding. Although field notes from this study often indicated with what broader action pattern a behavior was associated, the recording of that information was not consistent enough to allow its use in analysis. Future studies that need to incorporate more detailed elements of the sea otter behavioral ethogram may need further notes.

Also of consideration in behavioral development studies is whether behaviors occurring early in an animal's life are functionally and mechanically similar to those occurring later. Chalmers cautioned that "there is no guarantee that an early behaviour that is a precursor of a later one in its form or morphology is also its precursor in function." However, if research subjects are clearly marked and identifiable over time, then the observed behavior can be treated as a continuum, and the question of behavioral precursors is answered. As the individually recognized sea otter pups in this study were followed from birth until separation from their mothers, it can be assumed that early manifestations of a behavior were indeed "the same" as later ones. This replaces some of the doubt introduced by an earlier study (Sandegren et al. 1973) of unmarked otters, where each day's data had to be treated separately, and no continuum of behavioral development within a behavior could be assumed.

Application of findings of this study to broader contexts

The dynamic interactions between sea otter mothers and pups could be interpreted in terms of evolutionary significances of caretaking behavior. Other studies of captive and wild animals have shown that eating habits of the young may be influenced by association with caretakers (Harper 1970). This may be the case for sea otters as well. Indirect influences may result when the mother's diet affects the taste of the milk consumed by the pup, and direct influences could be determined by the food given to, or taken by, the pup. If the pup leaves the natal area after separation from the mother, its future success may depend largely on the "transferability" of food preferences developed while with the mother. This is especially critical if the areas occupied after separation have prey compositions radically different from the natal area. The level of mutual stimulation and reciprocity between and mother and her pup would also determine whether learned skills, like chest-pounding, would become part of the pup's behavioral repertoire. Future foraging (and reproductive) success would be directly affected.

An interesting future study would compare sea otters with other top marine carnivores (odontocete cetaceans, pinnipeds) in terms of skill acquisition by the young and the social context presented by each species. Each group provides a different model of caretaking; caretaking would influence the nature of skills needed or acquired, those skills in turn may determine the differential reproductive success of the young after they separate from the mother, and differential success circles back to analyses of the "success" of various social systems within the marine context.

Interesting comparisons of sea otters with terrestrial carnivores also could be made. Sea otters could be especially useful in comparisons with cats, with whom they share several social characteristics. Sea otters and most cats (excluding the lion) are considered solitary. Because all mammalian species are more or less social and regularly interact with others, being solitary does not exclude them from being social. Instead, solitary behavior is contrasted with cooperative behavior (Sandell 1989). Sea otters do not feed, groom, care for their young, or defend against predators in a cooperative manner. Each mother and her pup form a basic social unit. Sea otters are highly gregarious, and often rest in groups, but they do not "cooperate" in any of the contexts listed above. Kleiman and Eisenberg (1973) stated:

> "Primitive carnivores probably existed at rather low densities and were competing for food and space. Males and females may have occupied distinct home ranges, and these were defended from incursions by adults of either sex. The female reared her young alone, and the family split up during or shortly after weaning... A slight advance over this solitary and territorial condition may have occurred when one or more females' home ranges began to be encompassed by the home range of a single male. Under these conditions, an adult male could impregnate more than one female by excluding other males from the home range; he could reduce competition for resources utilized by pregnant and lactating females. In such solitary species, affiliative behaviour would only be seen during the parental rearing phase or at the mating season..." (p. 651)

Such systems are found today with bobcat, lynx, tiger, leopard, and puma. The social structure of the lion, the only social felid, revolves around a mother and her maturing daughters.

Upon separation from mothers, almost all male sea otter pups leave the natal area and travel to peripheral male areas (Loughlin 1980); some female pups also may move out of the natal area, and perhaps to the peripheral male groups, but most stay near the mothers. Some female pups remaining in their natal areas continue to interact with their mothers (Riedman pers. comm.). Sea otters do not as yet exhibit any cooperative behaviors, but continuing presence of daughters in their mothers areas offers an interesting question: Is the present social structure (based on solitary mother-young social units) in evolutionary transit to social groupings of mothers and daughters that would include more cooperative behaviors?

There are relatively few data on behavioral development of motor skills within the Carnivora (Bekoff 1989 and references therein). Gathering information on early development in sea otters is relatively easy. Similar data is much more difficult to gather for ranging pinnipeds or terrestrial cats, and is not yet available for the mustelids that den with their young. Proximate factors influencing ontogeny can be determined for sea otters, which can then form the basis for studies of comparative evolution of ontogenetic "trajectories" (Bekoff) by other carnivores.

Sea otters provide another advantage to studies on carnivores not readily available from other members of the order. There is a period in most carnivores between separation from the mother and attainment of sexual maturity. This time lag compounds difficulties in making long-term observations of identified individuals. Hind-flipper tags used in recent studies of sea otters are proving fairly persistent, and small radio transmitters that can be incorporated in them allow tracking of individuals over short time periods. Methods of capture also are being steadily refined. A persistent program of capture and tagging of pups before separation from their mothers has allowed data gathering on 12 weaned pups (Marianne Riedman, Monterey Bay Aquarium, pers. comm.). Further behavioral studies on known-age pups could be enhanced by incorporating a radio-tag in the flipper tag. A 30-day transmitter life would allow tracking of dispersing young and follow-up observations on success after separation. The foot-tags would be identifiable even after the transmitter failed, and observations could continue on the young otters until and beyond the time they reached sexual maturity. Differential success based on early ontogeny could be assessed more completely than may ever be possible for any other marine mammal or carnivore. Differential mortality by sex and age, and estimating possible influences on sex ratio by population density and degrees of exploitation, would give life history information critical to future decisions on fisheries management and oil exploration within the sea otter range.

The precise description of motor and social skills, and studies on their acquisition, is prerequisite for further research on behavior sequences. The integrated motor patterns developing from shorter sequences will turn into the coordinated acts of grooming, foraging, or social behavior. Ontogenetic studies in the sea otter of skills development, patterns, and their affect on future success opens the comparative door for similar understanding in other species.

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Table 1. Tag identification information of the eight mother otters included in this study and determination of estimated birthdates for the ten pups born during the study period.

Mother otter tag identification	Information from scans	Estimated birthdate
Red 40	Seen without pup 11 Mar. 1982 Seen with pup 16 Mar. 1982	13 Mar. 1982 (+/- 4 days)
Red 51	Seen without pup 6 April 1982 Seen with pup 12 April 1982	9 Apr. 1982 (+/- 4 days)
Dark Green 1453A (First of two pups)	Seen without pup 19 April 1982 Seen with pup 26 April 1982	22 Apr. 1982 (+/- 5 days)
Light Green 398A (First of two pups)	Seen without pup 1 May 1982 Seen with pup 3 May 1982	2 May 1982 (+/- 1 day)
Red 64	Seen without pup 30 August 1982 Seen with pup 16 September 1982	7 Sep. 1982 (+/- 9 days)
Dark Green 1454	Seen without pup 22 October 1982 Seen with pup 11 November 1982	31 Oct. 1982 (+/- 10 days)
Dark Green 1453B (Second of two pups)	Seen without pup 2 December 1982 Seen with pup 27 December 1982	20 Dec. 1982 (Est. 1 week old when first seen)
Red 43	Seen without pup 28 December 1982 Seen with pup 6 January 1983	1 Jan. 1983 (+/- 5 days)

Table 1, continued.

Mother otter tag identification	Information from scans	Estimated birthdate
Dark Green 1458	Seen without pup 10 January 1983 Seen with pup 15 January 1983	12 Jan. 1983 (+/- 3 days)
Light Green 398B (Second of two pups)	Seen without pup 10 June 1983 Seen with pup 17 June 1983	13 Jun. 1983 (+/- 5 days)

Table 2. Motor and social skills used to describe actions and interactions of mother, pup, and otters interacting with mother and/or pup. In parentheses following each behavior, M=mother, P=pup, O=other otter, M/P=mother/pup pair. Equivalent terms used by Packard et al. (1981) are given.

This study	Packard et al. 1981
Resting quiet (M,P)	Floating, low intensity
Resting alert (M,P)	Floating, high intensity
Groom self (M)	
Groom by rubbing (P)	Rubbing
Groom by stroking (P)	Stroking
Groom by licking (P)	Nibble or lick
Groom by lateral roll (P)	Logroll
Groom by shoulder roll (P)	Tuckroll
Groom by forward roll (P)	Somersault
Groom by hanging (P)	Hanging
Groom by bubbling (P)	
Groom by headshake (P)	Shake
Groom pup (M)	
Groom mother (P)	
Travel on dorsum (M,P)	Sculling
Travel on ventrum (M,P)	Swimming, porpoising
Nurse (M)	Suckle
Periscope (M,P)	Periscope
Dive (M)	Dive
Dive, non-foraging (P)	
Dive, foraging (P)	
Manipulate food (M)	Eating
Mani. food without consumption (P)	
Mani. food with consumption (P)	
Chest pound (P)	Pounding
Give food to pup (M)	
Take food from mom (P)	
Feeding intertidally (M)	
Vocalize (M,P)	
Environmental exploration (P)	
Unspecified "active" (P)	
Mother approach (directed to P,O)	
Mother proximity (directed to P,O)	
Mother contact (directed to P,O)	
Pup approach (directed to M,O)	
Pup proximity (directed to M,O)	
Pup contact (directed to M,O)	

Table 2, continued.

This study	Packard et al. 1981
Other approach (directed to M,P,M/P)	
Other proximity (directed to M,P,M/P)	
Other contact (directed to M,P,M/P)	
Mother/pup pair approach (directed to O)	
Mother/pup pair proximity (directed to O)	
Mother/pup pair contact (directed to O)	

Table 3. Definitions of behaviors recorded for sea otter pups.

Behaviors initiated by pup	Definition or application
<u>Resting</u>	
Resting quiet	Lying still with eyes closed for 10 seconds or more.
Resting alert	Animal may be quiescent, but eyes are open. May apply also to otters that are pausing in activity, especially one attributable to another category.
<u>Grooming</u>	
Groom by rubbing	Repeatedly brushing one hind foot against the other; motion acts to work water out of the fur, lift fur, and work air back in between hairs. May function also to move wax up the hair shaft.
Groom by stroking	Using forepaws to work water out of fur along all parts of body; the motion acts also to lift fur, move air back in between hairs, move wax along hair shaft.
Groom by licking	Using tongue to lick water off fur along any part of body.
Groom by lateral rolling	Otter's whole body turns around its longitudinal axis. Used to work debris out of fur and air back in.

Table 3, continued.

Behaviors initiated by pup	Definition or application
<u>Grooming, continued</u>	
Groom by shoulder rolling	This roll is led by one shoulder, with rest of body following along a line transverse with the back. Functions to remove debris from fur and work air back in.
Groom by forward rolling	This roll is led by the head, and follows a line going directly down the back, much like a somersault. Like other rolls, it acts to remove debris and work air back into fur.
Groom by hanging	Otter curls forward into water, leaving curve of back exposed on surface. Without rolling, otter remains with head submerged for extended period of time. Tail and hind feet also may be below water's surface. Position presumably used for underwater stroking of fur for more forceful cleaning and aeration.
Groom by bubbling	Using hanging position, otter forcefully blows a lungfull of air into fur (a good view of the otter also will show the bubbles of air breaking the water's surface next to it). This action is especially good for forcing air back into fur along otter's ventral surface. Otter will lift head to water's surface to get a fresh breath of air to repeat bubbling.

Table 3, continued.

Behaviors initiated by pup	Definition or application
<u>Grooming, continued</u>	
Groom by headshake *	Fairly vigorous shaking of head from side to side, presumably used to clear water from the ears, face, or head fur.
Groom mother	This is a general grooming category that can involve stroking, licking, or a general "mouthing" of some part of the mother's body. Tactile manipulations of the mother by the pup that were not clearly seen but were presumed to be grooming also were included in this category.
<u>Travel</u>	
Travel dorsal	Otter swims on its back, with forepaws held up against its chest. Otter may occasionally lean its head back to look into water or turn it to side to get a sense of direction. Hind feet are used for propulsion, and the tail may be used for steering. Sometimes only one hind foot is used for kicking. "Sculling" (swishing tail from side to side for propulsion) also is included in this category.
Travel ventral	Otter swims on belly, head pointed forward. Forepaws are folded back against chest, kicking hind feet provide propulsion. Tail trails behind and may aid in steering.

* This behavior scored for frequency only.

Table 3, continued.

Behaviors initiated by pup	Definition or application
<u>Feeding/Foraging</u>	
Suckle	Pup in suckling position and presumed to be suckling. Pup can be lying entirely on the reclining mother's belly, or lying in water perpendicular to mother with only head and neck reaching over to mother's nipples.
Periscope *	Otter temporarily assumes and maintains a vertical position in water, with head and shoulders above surface and rest of body below. Attitude is one of alertness, and behavior is used for visual scanning and listening. It often precedes a dive.
Dive	Otter makes a deliberate effort to submerge its entire body. Depending on the depth of dive and energy of otter, some of force necessary to drive it below the surface may come from arcing out of water just before the dive. Deeper dives are generally preceded by high arcs or "porpoises". Dive lasts for many seconds, or a minute or longer; prolonged submersion separates it from forms of ventral locomotion along water's surface that also may involve some arcing and/or shallow submersion.

* This behavior scored for frequency only.

Table 3, continued.

Behaviors initiated by pup	Definition or application
<u>Feeding/Foraging, continued</u>	
Manipulate food with consumption	Food is handled by forepaws and then carried to the mouth. Biting a food item apart and chewing also may be seen.
Manipulate food without consumption	A food item is handled by forepaws and perhaps mouthed, but no consumption of food is observed. Pups sometimes appear to want to eat the prey, but their inexperience (especially with hard-shelled prey) keeps them from successfully breaking into it. At other times, a pup may appear more interested in playing with food than eating it.
Chest pound *	Otter uses a tool (i.e., a shell, rock, or other hard item) to either pound against a food item or to use as an "anvil" against which prey can be pounded. A complete and correct chest pound involves successful use of both an appropriate prey item and an appropriate tool.
Take food from mother *	Pup reaches over to the mother and deliberately takes food from her mouth or paws.

* This behavior scored for frequency only.

Table 3, continued.

Behaviors initiated by pup	Definition or application
<u>Miscellaneous actions</u>	
Play	A general class of interactions that may include romping, tumbling and play-biting; these behaviors do not appear to be directed toward any other more specific end, such as feeding, grooming or locomotion.
Vocalize *	In-air sounds attributed to pup if it could be seen making the sounds at roughly the same time they were being heard by the observer. Most vocalizations heard from shore were high-pitched, high-energy screams used by the pup when it was separated from its mother. Otters also can make softer coos and gruff barks, but these generally cannot be heard by the shore-based observer.
Environmental exploration	Generally reserved for cases of manipulation of objects not considered regular food items. An example would be prolonged play/manipulation of a strand of kelp.
Unspecified "active"	A general category used when the pup was engaging in such a number of behaviors at such a rapid pace that they could not be separately and accurately timed. This category also would be used if the behavior engaged in by the pup was not one regularly included in this study.

* This behavior scored for frequency only.

Table 4. Amount of observation time (minutes, percent of total minutes) spent in each age interval.

Age interval	Inclusive weeks	Inclusive days	Minutes	Percent of total minutes
1	1-2	1-14	632.62	10.51
2	3-4	15-28	693.90	11.52
3	5-6	29-42	947.80	15.74
4	7-8	43-56	665.87	11.06
5	9-10	57-70	904.70	15.02
6	11-12	71-84	377.27	6.27
7	13-14	85-98	668.72	11.11
8	15-20	99-140	656.20	10.90
9	21-26	141-182	474.53	7.88

Table 5. Amount of observation time (minutes, percent of total minutes) spent on each pup.

Mother I.D. number	Minutes under observation	Percent of total minutes
Red 40	1557.08	25.86
Red 51	1542.27	25.61
Red 64	1083.55	17.99
Red 43	570.43	9.47
Light Green 398A	515.87	8.57
Light Green 398B	257.58	4.31
Dark Green 1458	166.37	2.76
Dark Green 1453A *	136.87	2.27
Dark Green 1454	100.83	1.67
Dark Green 1453B	88.75	1.47

* Disappeared after 51 days and presumably died.

Table 6. Portion of observation time (minutes, percent of total minutes) in each age interval pup considered "active".

Age interval	Minutes "active"	Percent of total minutes
1	174.42	27.57
2	282.23	40.67
3	487.98	51.49
4	379.28	56.96
5	545.30	60.27
6	305.40	80.95
7	259.97	38.88
8	586.52	89.38
9	279.02	58.80

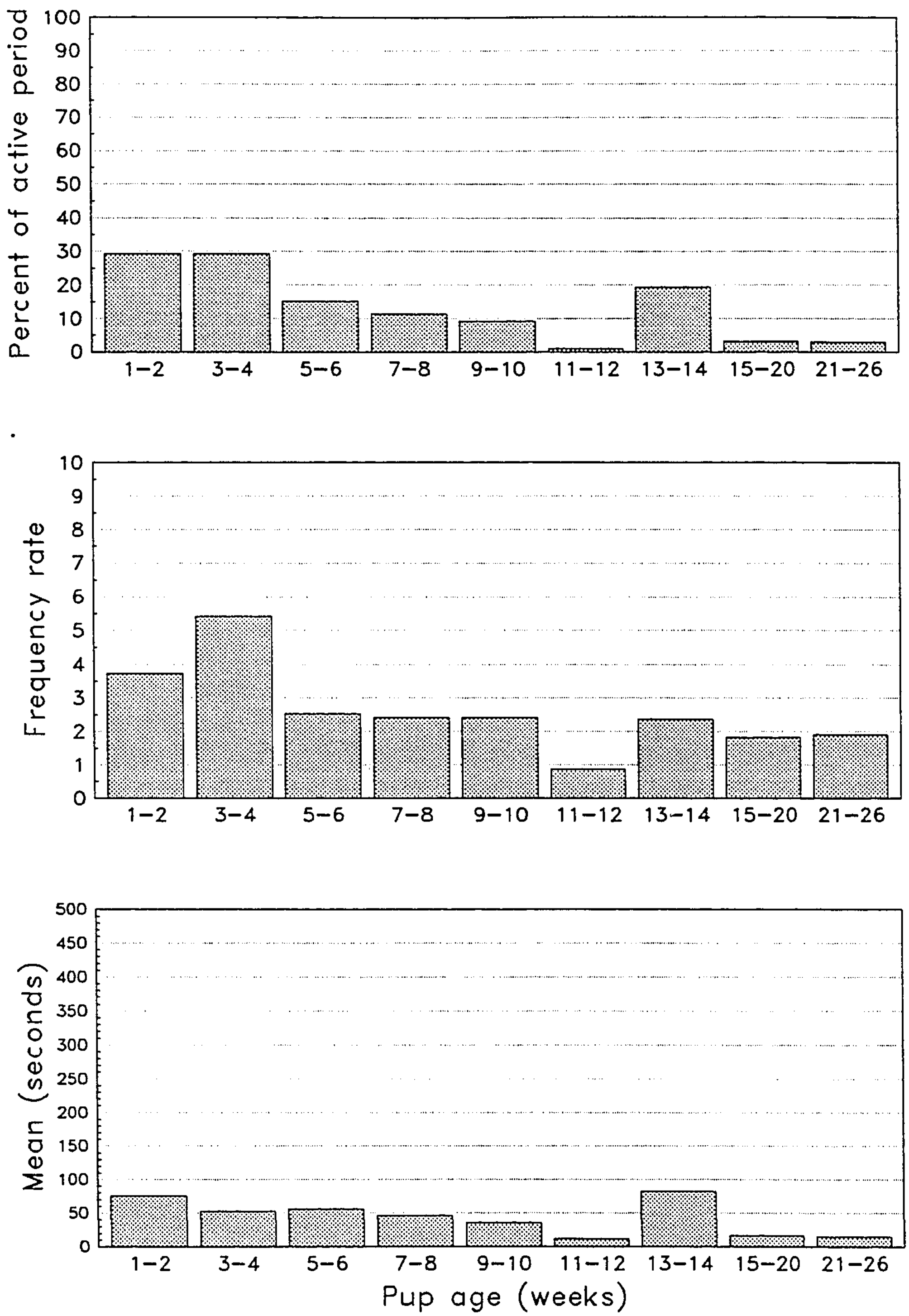
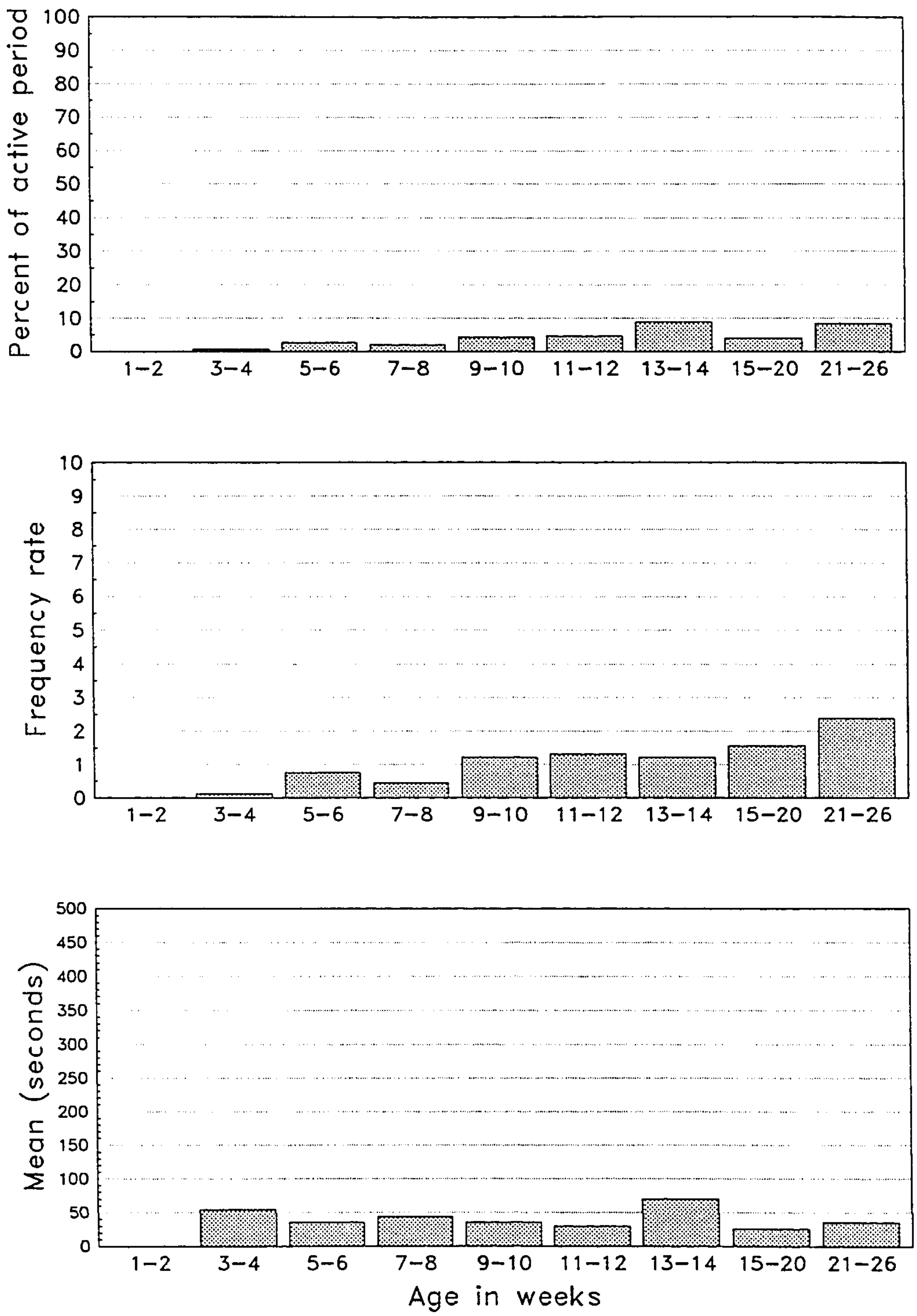

Percent of active period
100
90
80
70
60
50
40
30
20
10
0
1–2
3–4
5–6
7–8
9–10
11–12
13–14
15–20
21–26
Frequency rate
10
9
8
7
6
5
4
3
2
1
0
1–2
3–4
5–6
7–8
9–10
11–12
13–14
15–20
21–26
Mean (seconds)
500
450
400
350
300
250
200
150
100
50
0
1–2
3–4
5–6
7–8
9–10
11–12
13–14
15–20
21–26
Pup age (weeks)

Fig. 1


Percent of active period
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90
80
70
60
50
40
30
20
10
0
1–2
3–4
5–6
7–8
9–10
11–12
13–14
15–20
21–26
Frequency rate
10
9
8
7
6
5
4
3
2
1
0
1–2
3–4
5–6
7–8
9–10
11–12
13–14
15–20
21–26
Mean (seconds)
500
450
400
350
300
250
200
150
100
50
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1–2
3–4
5–6
7–8
9–10
11–12
13–14
15–20
21–26
Age in weeks

Fig. 2

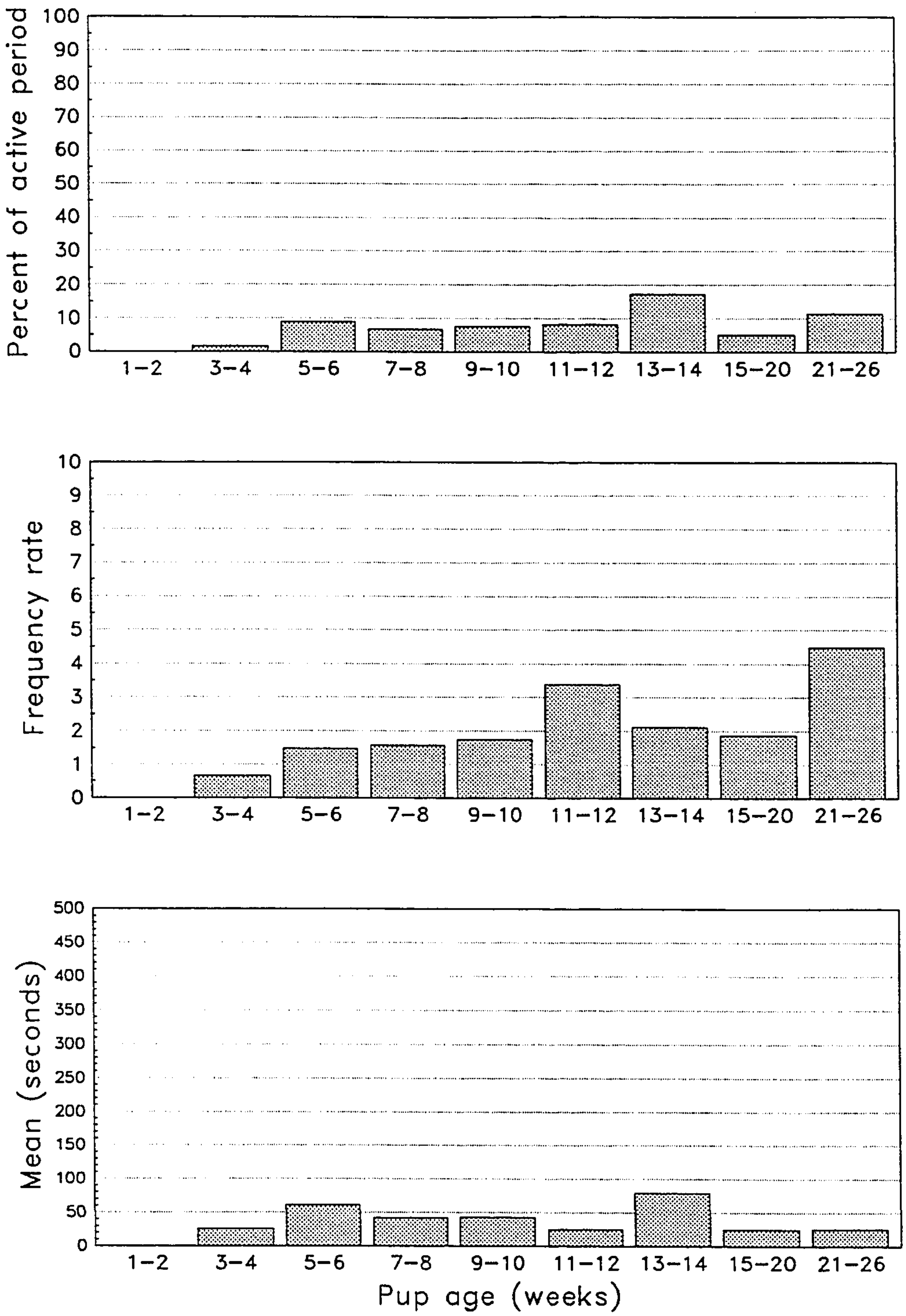
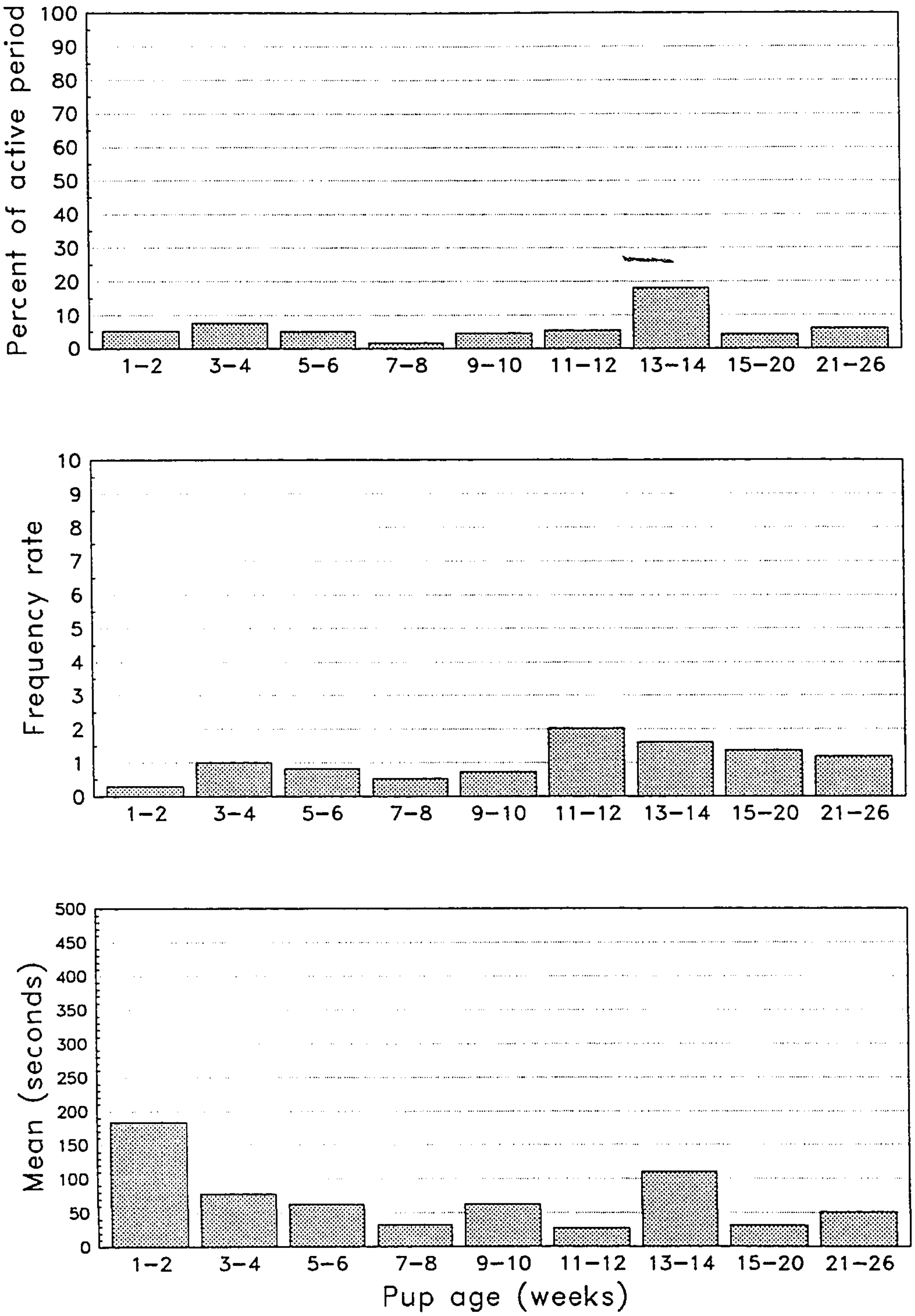

Percent of active period
100
90
80
70
60
50
40
30
20
10
0
1−2
3−4
5−6
7−8
9−10
11−12
13−14
15−20
21−26
Frequency rate
10
9
8
7
6
5
4
3
2
1
0
1−2
3−4
5−6
7−8
9−10
11−12
13−14
15−20
21−26
Mean (seconds)
500
450
400
350
300
250
200
150
100
50
0
1−2
3−4
5−6
7−8
9−10
11−12
13−14
15−20
21−26
Pup age (weeks)

Fig. 3


Percent of active period
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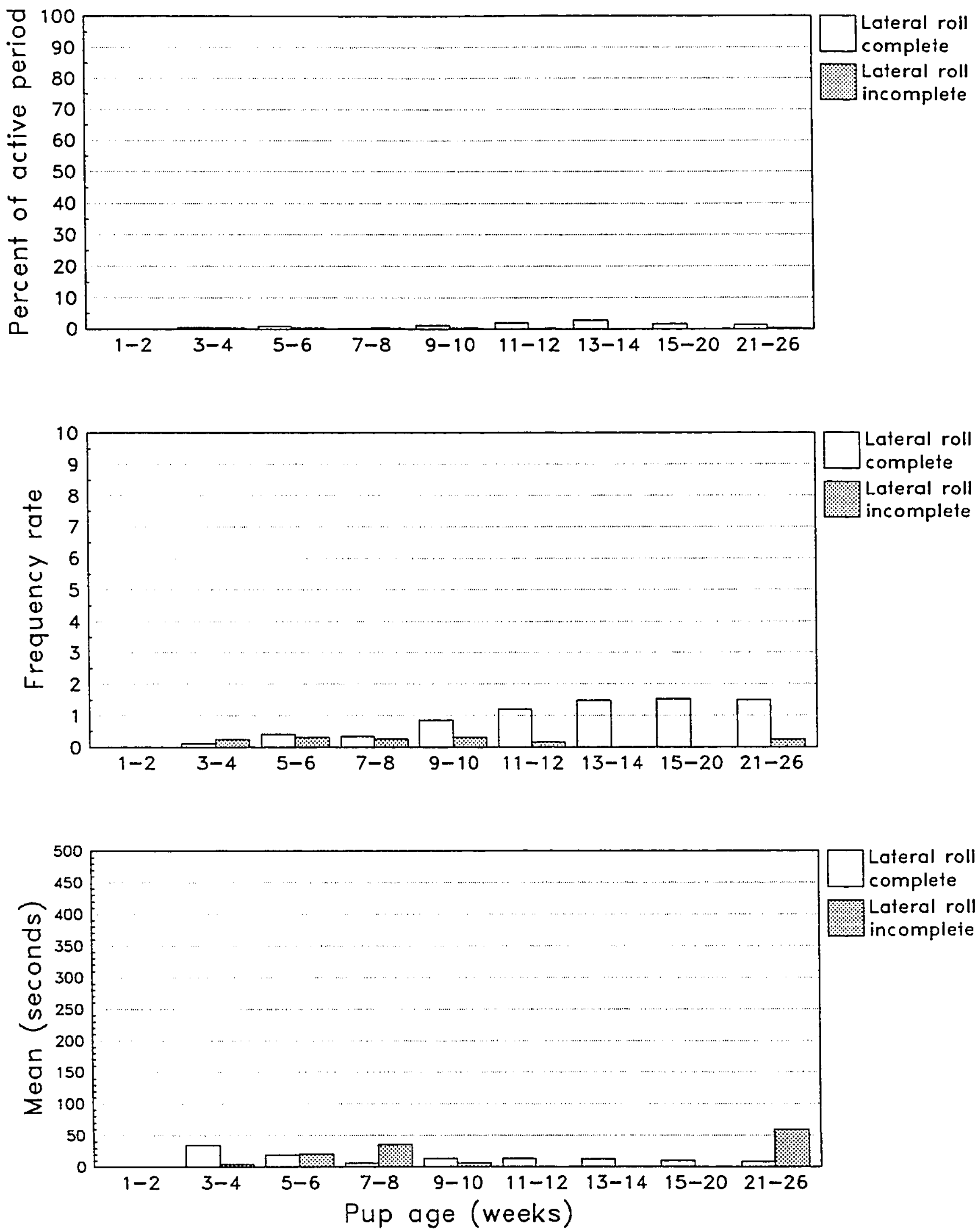
90
80
70
60
50
40
30
20
10
0
1-2
3-4
5-6
7-8
9-10
11-12
13-14
15-20
21-26
Frequency rate
10
9
8
7
6
5
4
3
2
1
0
Mean (seconds)
500
450
400
350
300
250
200
150
100
50
0
Pup age (weeks)

Fig. 4


Percent of active period
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90
80
70
60
50
40
30
20
10
0
1-2
3-4
5-6
7-8
9-10
11-12
13-14
15-20
21-26
Lateral roll complete
Lateral roll incomplete
Frequency rate
10
9
8
7
6
5
4
3
2
1
0
1-2
3-4
5-6
7-8
9-10
11-12
13-14
15-20
21-26
Lateral roll complete
Lateral roll incomplete
Mean (seconds)
500
450
400
350
300
250
200
150
100
50
0
1-2
3-4
5-6
7-8
9-10
11-12
13-14
15-20
21-26
Pup age (weeks)
Lateral roll complete
Lateral roll incomplete

Fig. 5

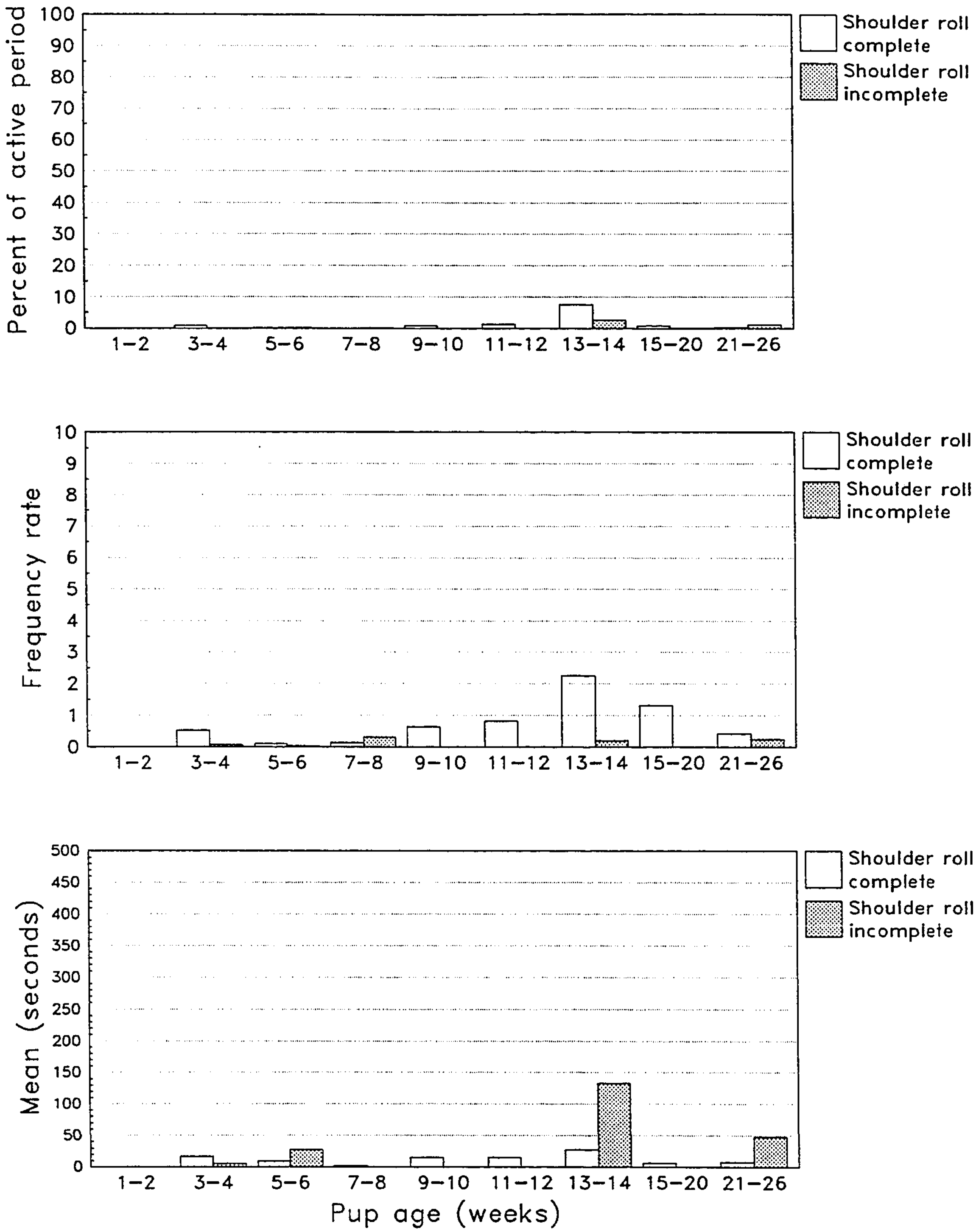
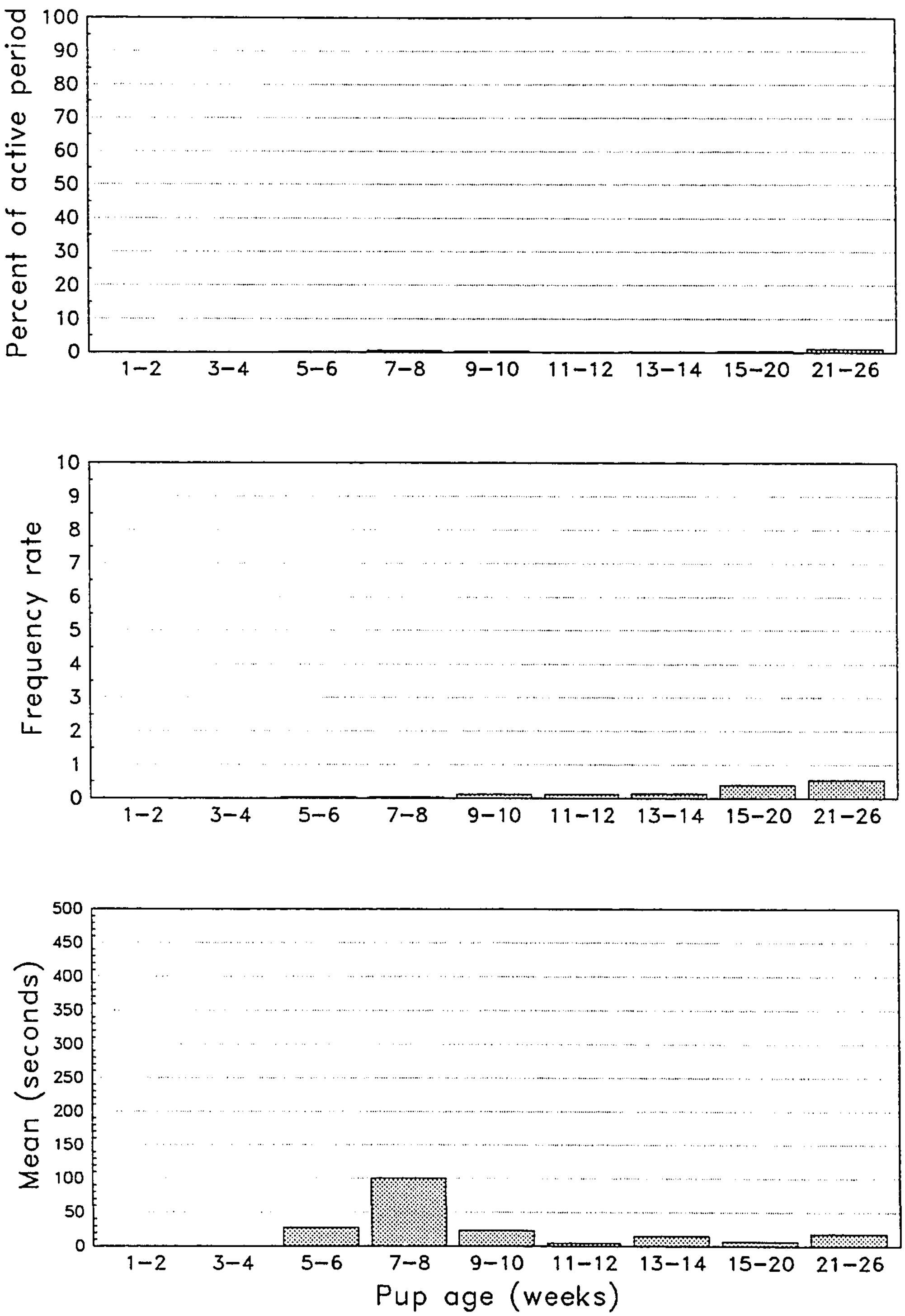

Percent of active period
100
90
80
70
60
50
40
30
20
10
0
1−2
3−4
5−6
7−8
9−10
11−12
13−14
15−20
21−26
Shoulder roll complete
Shoulder roll incomplete
Frequency rate
10
9
8
7
6
5
4
3
2
1
0
1−2
3−4
5−6
7−8
9−10
11−12
13−14
15−20
21−26
Shoulder roll complete
Shoulder roll incomplete
Mean (seconds)
500
450
400
350
300
250
200
150
100
50
0
1−2
3−4
5−6
7−8
9−10
11−12
13−14
15−20
21−26
Pup age (weeks)
Shoulder roll complete
Shoulder roll incomplete

Fig. 6


Percent of active period
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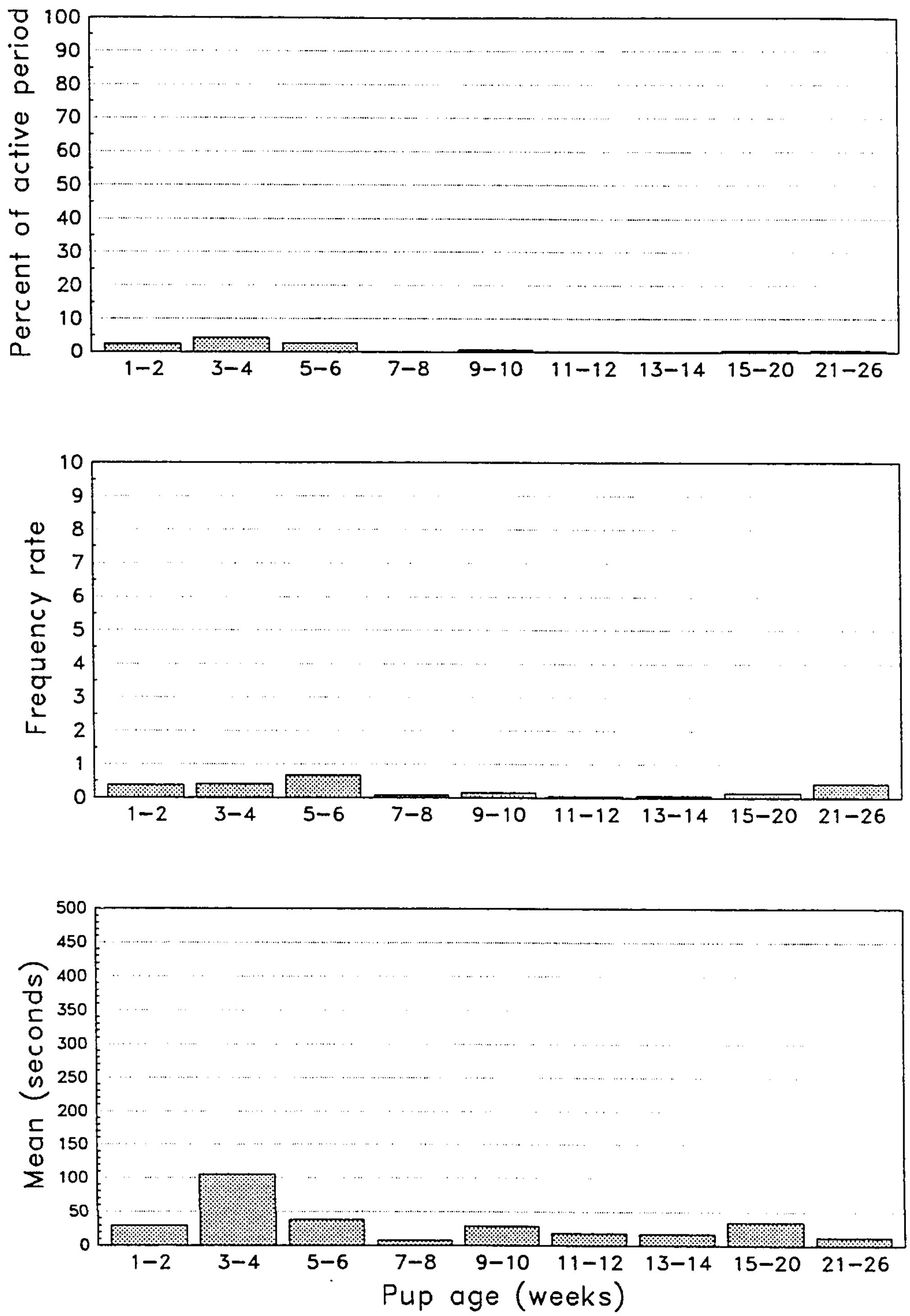
90
80
70
60
50
40
30
20
10
0
1−2
3−4
5−6
7−8
9−10
11−12
13−14
15−20
21−26
Frequency rate
10
9
8
7
6
5
4
3
2
1
0
Mean (seconds)
500
450
400
350
300
250
200
150
100
50
0
Pup age (weeks)

Fig. 7


Percent of active period
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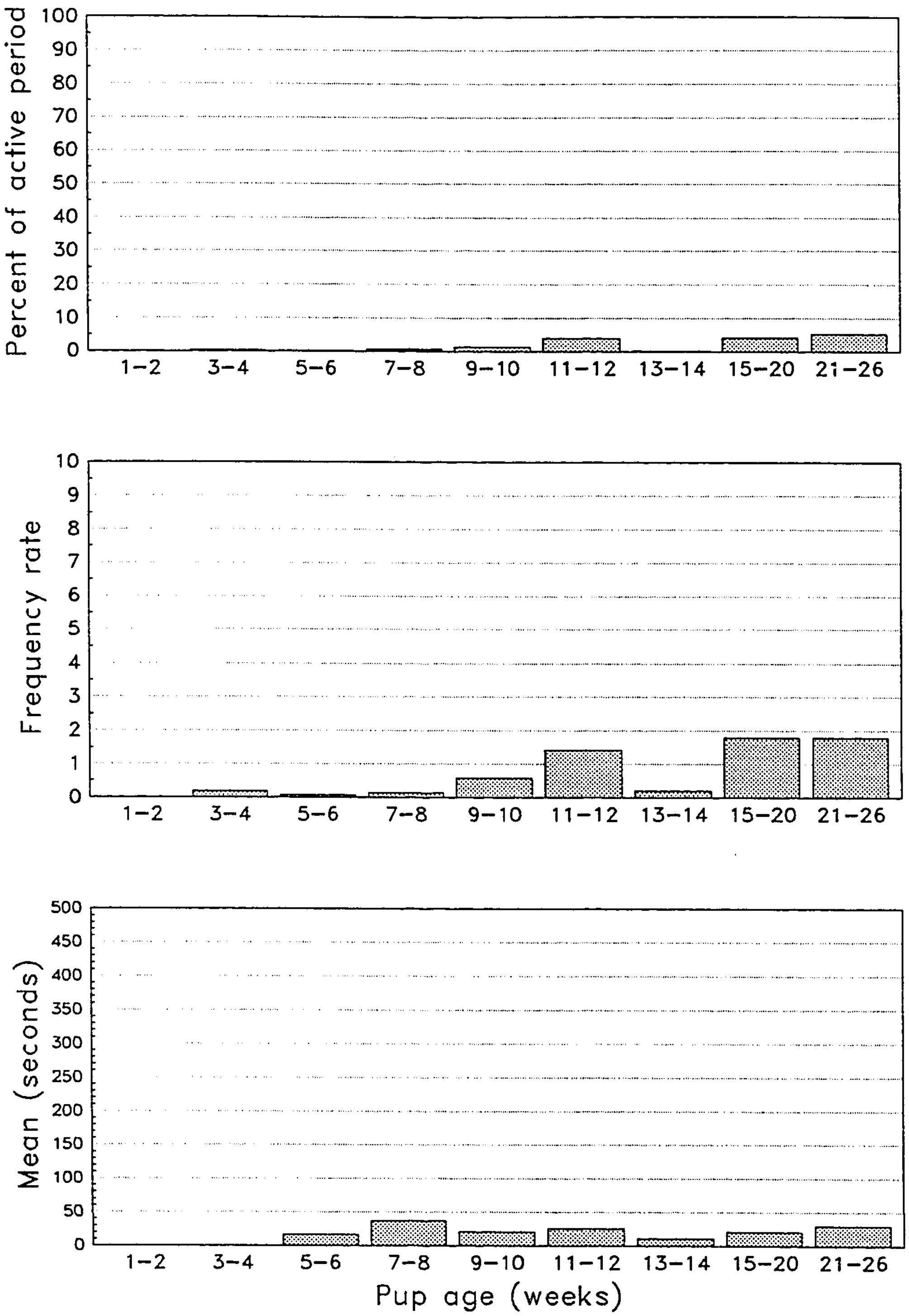
90
80
70
60
50
40
30
20
10
0
1−2
3−4
5−6
7−8
9−10
11−12
13−14
15−20
21−26
Frequency rate
10
9
8
7
6
5
4
3
2
1
0
1−2
3−4
5−6
7−8
9−10
11−12
13−14
15−20
21−26
Mean (seconds)
500
450
400
350
300
250
200
150
100
50
0
1−2
3−4
5−6
7−8
9−10
11−12
13−14
15−20
21−26
Pup age (weeks)

Fig. 8


Percent of active period
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70
60
50
40
30
20
10
0
1–2
3–4
5–6
7–8
9–10
11–12
13–14
15–20
21–26
Frequency rate
10
9
8
7
6
5
4
3
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1
0
Mean (seconds)
500
450
400
350
300
250
200
150
100
50
Pup age (weeks)

Fig. 9

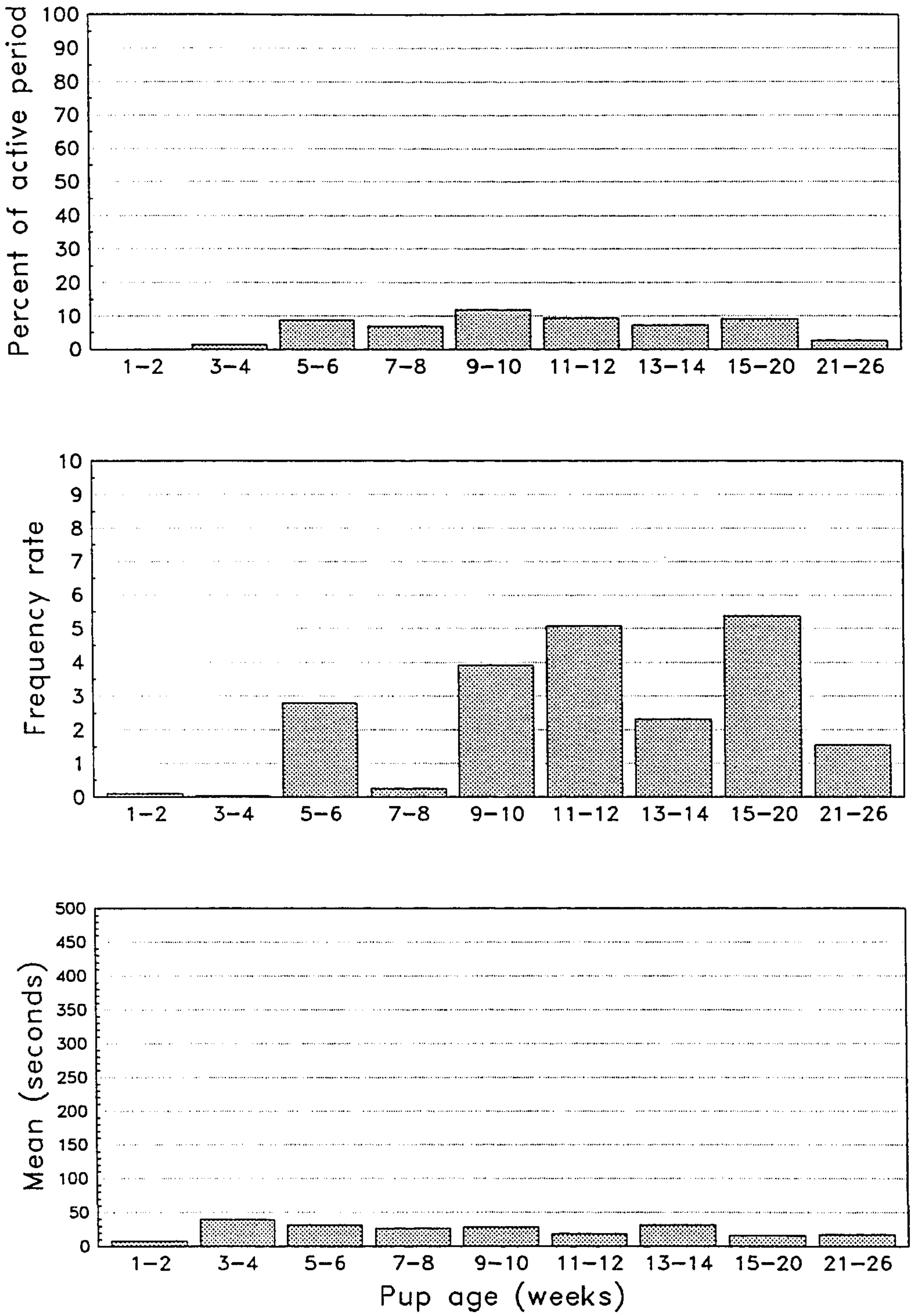

Percent of active period
100
90
80
70
60
50
40
30
20
10
0
1–2
3–4
5–6
7–8
9–10
11–12
13–14
15–20
21–26
Frequency rate
10
9
8
7
6
5
4
3
2
1
0
1–2
3–4
5–6
7–8
9–10
11–12
13–14
15–20
21–26
Mean (seconds)
500
450
400
350
300
250
200
150
100
50
0
1–2
3–4
5–6
7–8
9–10
11–12
13–14
15–20
21–26
Pup age (weeks)

Fig. 10

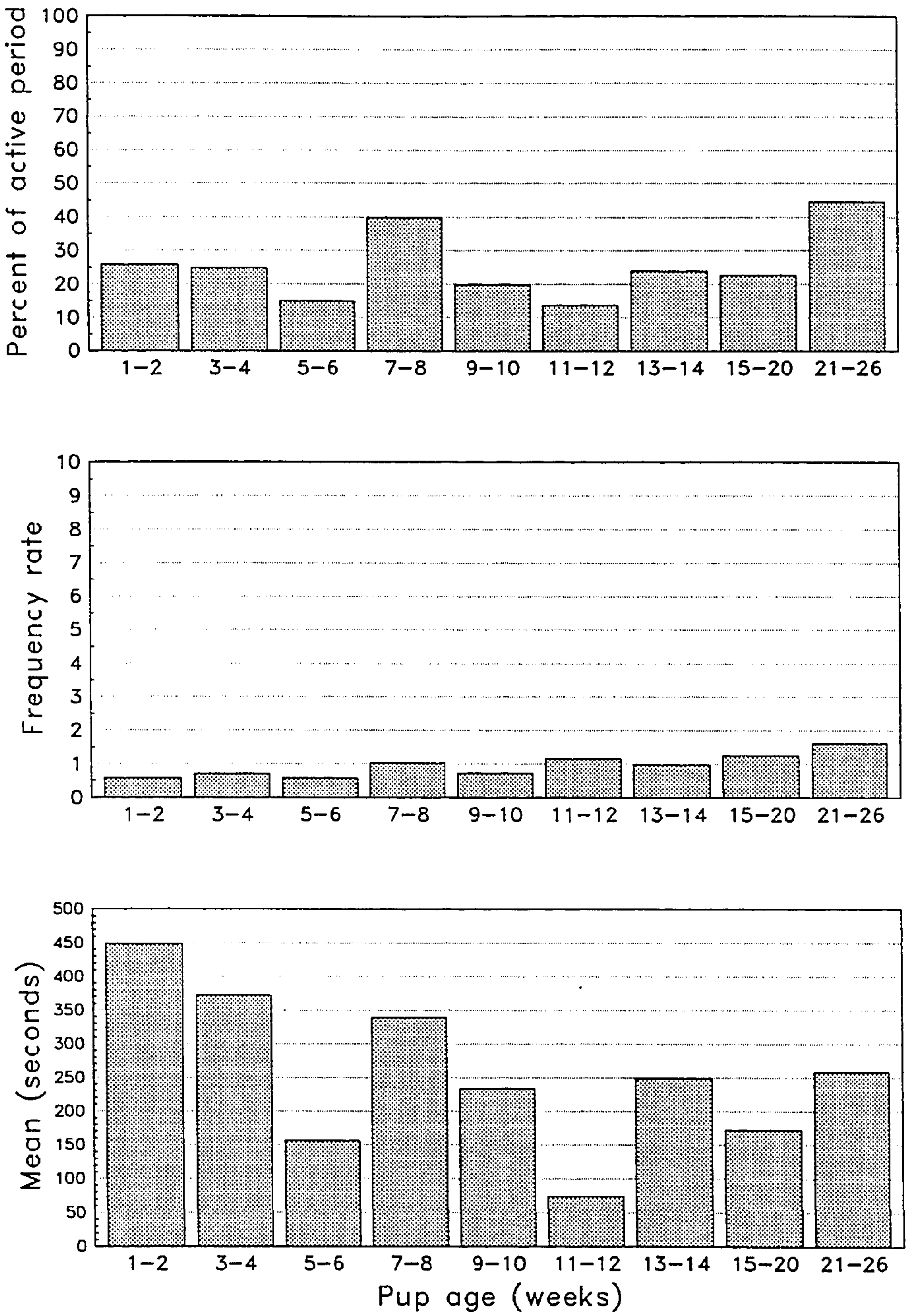

Percent of active period
100
90
80
70
60
50
40
30
20
10
0
1–2
3–4
5–6
7–8
9–10
11–12
13–14
15–20
21–26
Frequency rate
10
9
8
7
6
5
4
3
2
1
0
1–2
3–4
5–6
7–8
9–10
11–12
13–14
15–20
21–26
Mean (seconds)
500
450
400
350
300
250
200
150
100
50
0
1–2
3–4
5–6
7–8
9–10
11–12
13–14
15–20
21–26
Pup age (weeks)

Fig. 11

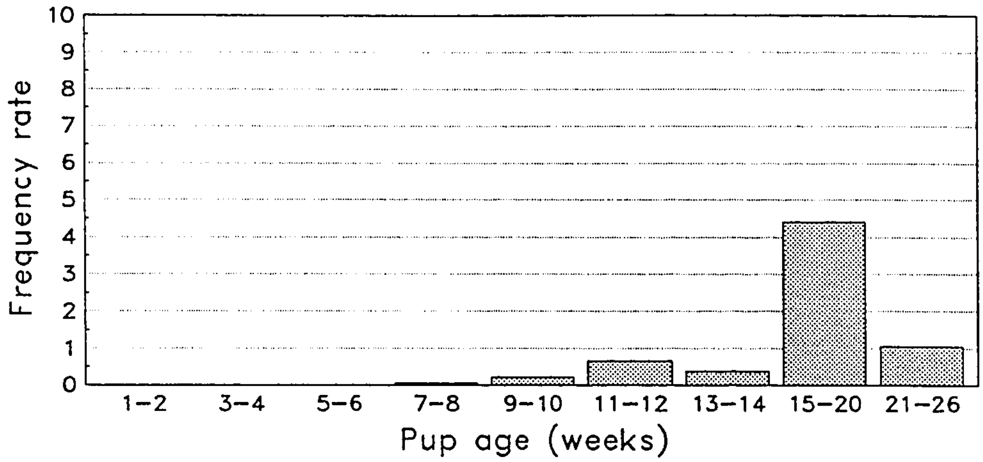

10
9
8
7
6
5
4
3
2
1
0
Frequency rate
1–2
3–4
5–6
7–8
9–10
11–12
13–14
15–20
21–26
Pup age (weeks)

Fig. 12

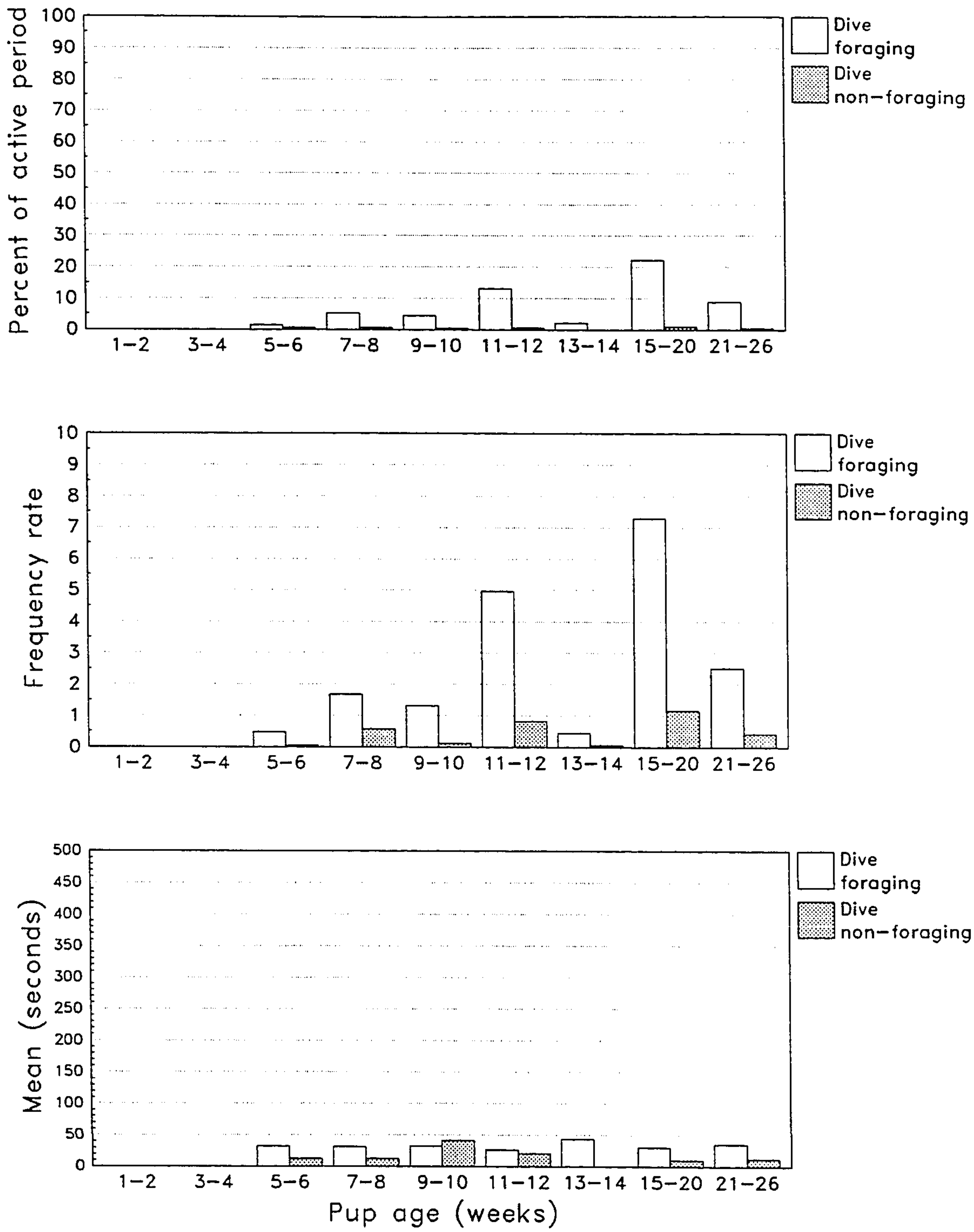

Percent of active period
100
90
80
70
60
50
40
30
20
10
0
1-2
3-4
5-6
7-8
9-10
11-12
13-14
15-20
21-26
Dive foraging
Dive non-foraging
Frequency rate
10
9
8
7
6
5
4
3
2
1
0
Mean (seconds)
500
450
400
350
300
250
200
150
100
50
Pup age (weeks)

Fig. 13

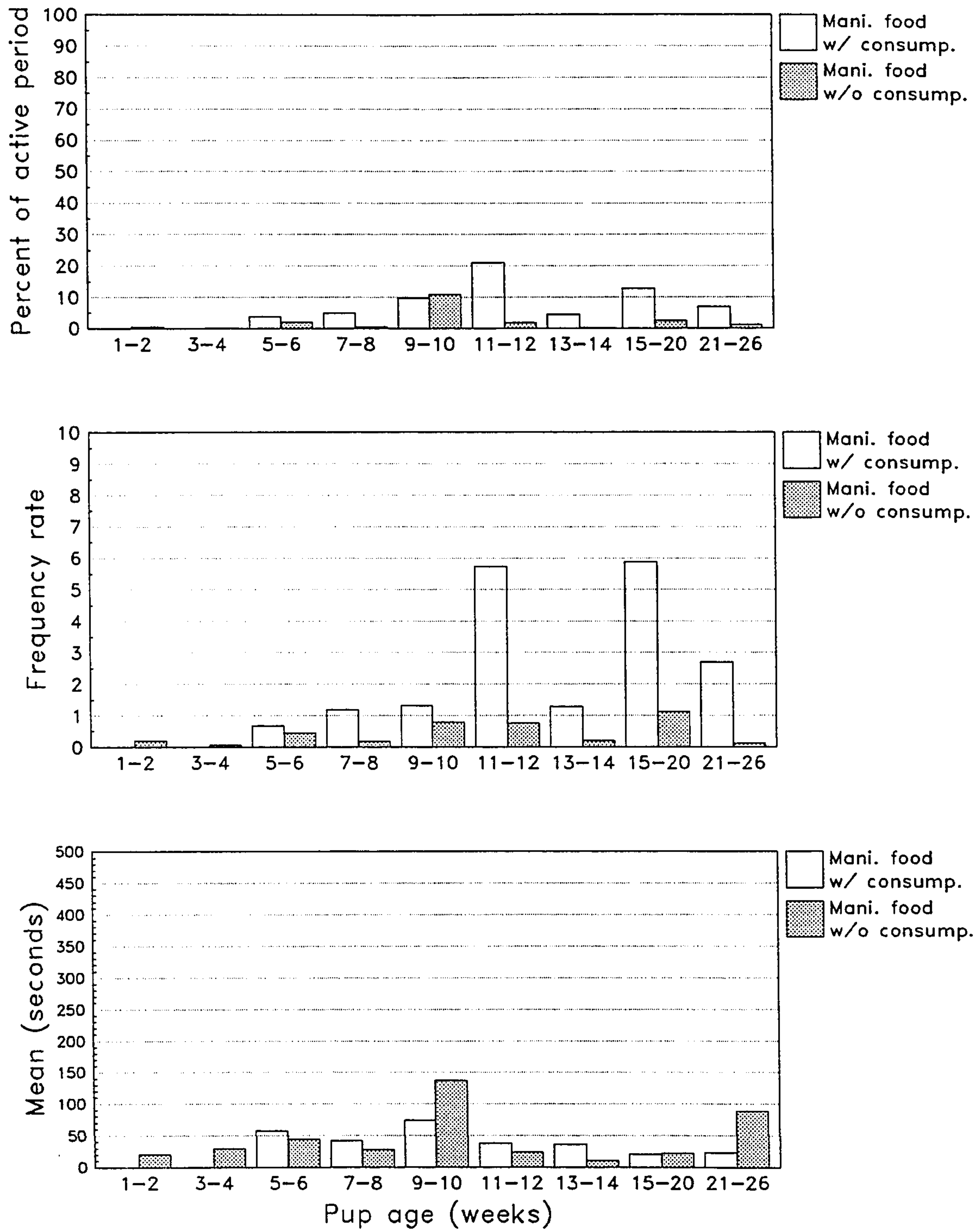

100
90
80
70
60
50
40
30
20
10
0
Percent of active period
1-2
3-4
5-6
7-8
9-10
11-12
13-14
15-20
21-26
Mani. food w/ consump.
Mani. food w/o consump.
10
9
8
7
6
5
4
3
2
1
0
Frequency rate
Mani. food w/ consump.
Mani. food w/o consump.
500
450
400
350
300
250
200
150
100
50
0
Mean (seconds)
Mani. food w/ consump.
Mani. food w/o consump.
Pup age (weeks)

Fig. 14

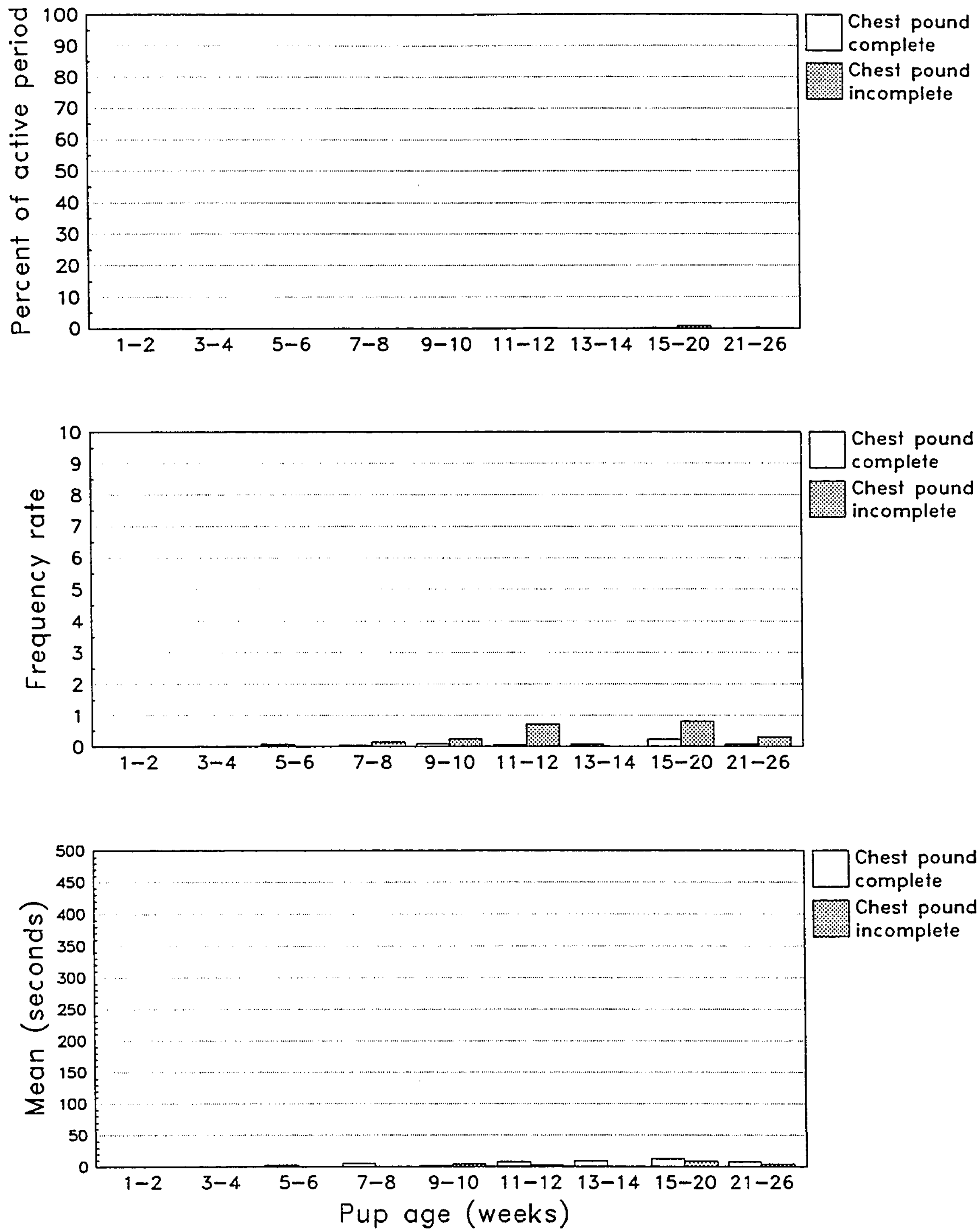

Percent of active period
100
90
80
70
60
50
40
30
20
10
0
1-2
3-4
5-6
7-8
9-10
11-12
13-14
15-20
21-26
Chest pound complete
Chest pound incomplete
Frequency rate
10
9
8
7
6
5
4
3
2
1
0
Mean (seconds)
500
450
400
350
300
250
200
150
100
50
0
Pup age (weeks)

Fig. 15

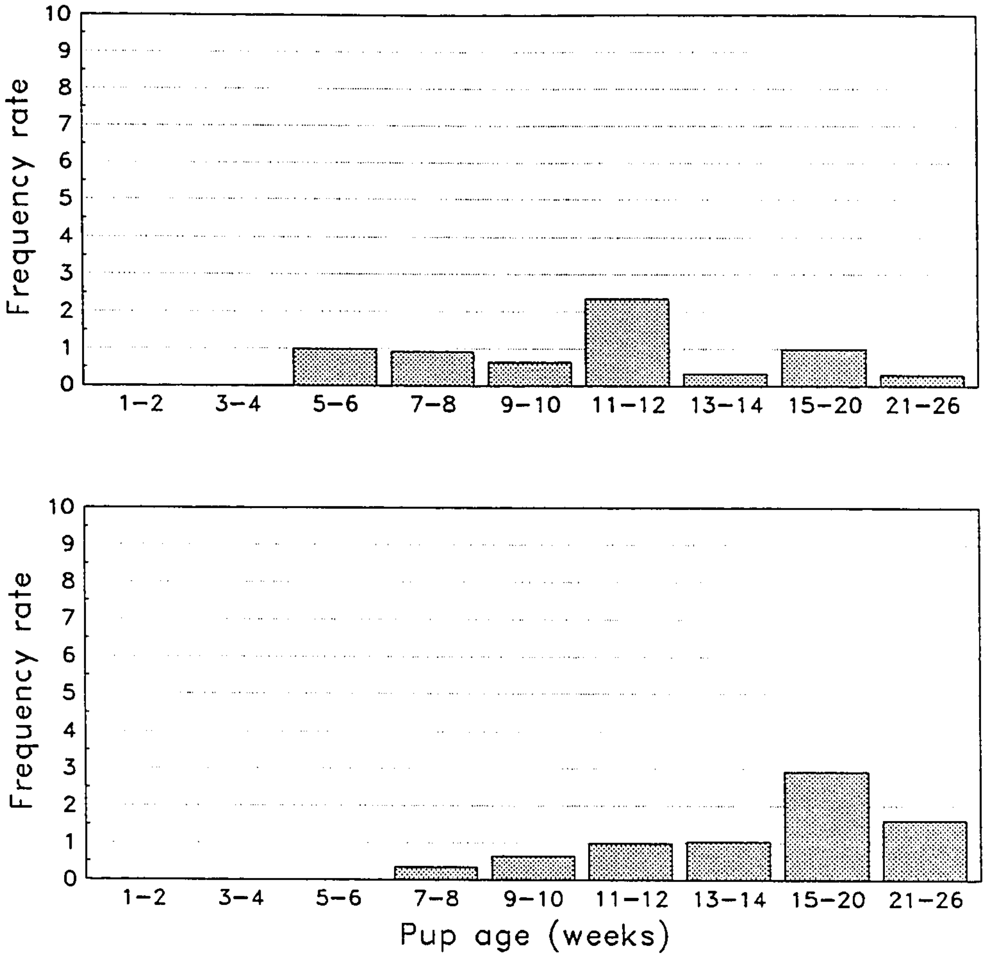
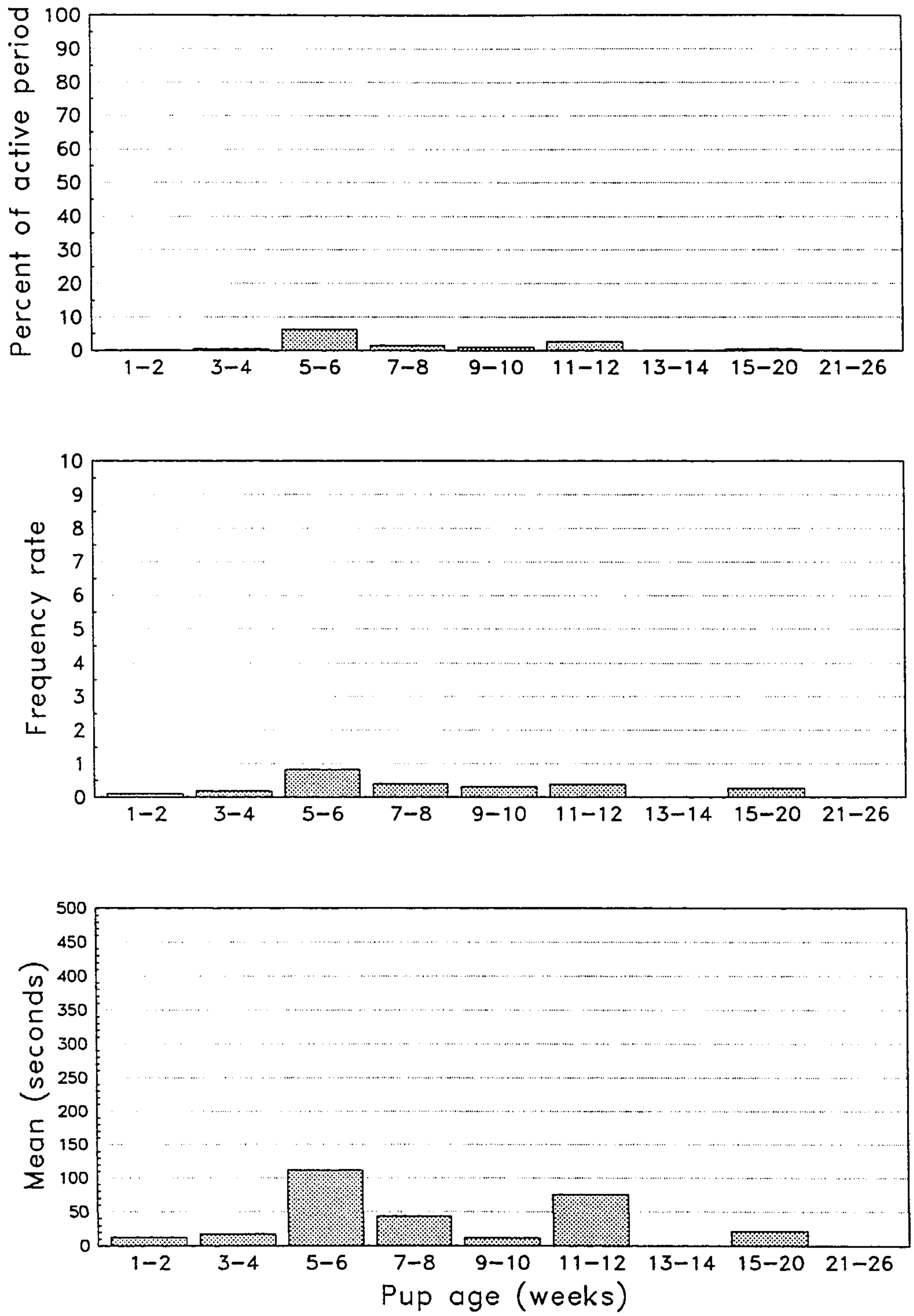

Frequency rate
10
9
8
7
6
5
4
3
2
1
0
1–2
3–4
5–6
7–8
9–10
11–12
13–14
15–20
21–26
Frequency rate
10
9
8
7
6
5
4
3
2
1
0
1–2
3–4
5–6
7–8
9–10
11–12
13–14
15–20
21–26
Pup age (weeks)

Fig. 16



Percent of active period
100
90
80
70
60
50
40
30
20
10
0
1-2
3-4
5-6
7-8
9-10
11-12
13-14
15-20
21-26
Frequency rate
10
9
8
7
6
5
4
3
2
1
0
Mean (seconds)
500
450
400
350
300
250
200
150
100
50
0
Pup age (weeks)

Fig. 17

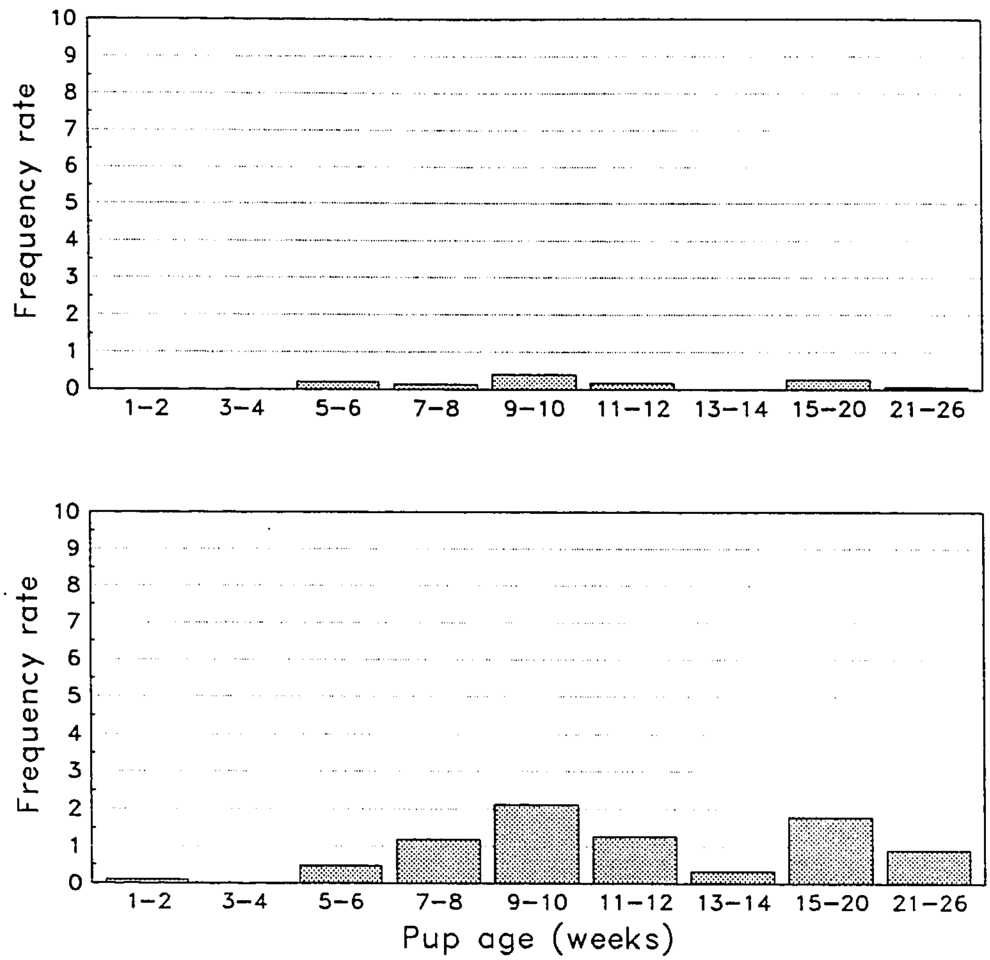

Frequency rate
10
9
8
7
6
5
4
3
2
1
0
1−2
3−4
5−6
7−8
9−10
11−12
13−14
15−20
21−26
Frequency rate
10
9
8
7
6
5
4
3
2
1
0
1−2
3−4
5−6
7−8
9−10
11−12
13−14
15−20
21−26
Pup age (weeks)

Fig. 18

Appendix 1. Information categories recorded for each sea otter seen during periodic scans.

Category	Definition or application
Date	
Observation period	Time group first observed until the time the data on last otter in group was recorded.
Tag information	Color and position of tags on tagged otters; other otters noted as "Not tagged" or "Feet not seen".
Location	Recorded from 100 m^2 grid overlays on area maps, and with coastal landmark mnemonics.
Position relative to kelp	Recorded as: Open water nearshore, inner edge of kelp bed, middle of kelp bed, outer edge of kelp bed, open water offshore of kelp, associated with single kelp plant.
Position relative to shore	Describes the degree of protection from rough water or strong wind. Recorded as: Protected, moderately protected, moderately exposed, or exposed.
Beaufort sea condition	Often recorded both for conditions offshore the kelp beds and for those within the beds.
Distance from shore (m)	Estimated perpendicular distance from observer to otter

Appendix 1, continued.

Category	Definition or application
Wind direction	
Percent cloud cover	
Air temperature	Degrees Fahrenheit
Sex and life stage	Recorded as: Adult (and as male or female, if discernible), female with small pup (dependent pup with natal pelage), or female with large pup (dependent pup with adult pelage)
Head color	Recorded as: Dark, lightly grizzled, heavily grizzled, or white.
Nose condition	Often indicative, with females, of recent mating activity. Recorded as: Dark nose pad, nose with white/healed scar, nose with pink/healed scar, nose with red/open wound.
General behavior when first observed	Recorded as: Resting, grooming, feeding, swimming, or interacting
Names of observers	
Other comments	

Appendix 2. Percent of active period, frequency rate and sample size (n) used in their calculations for each behavior and each age interval.

Age in weeks	1-2			3-4			5-6		
	%	fr	n	%	fr	n	%	fr	n
Resting quiet	72.43	1.19	45	59.33	0.94	39	48.51	0.91	52
Resting alert	8.06	1.03	39	11.92	2.21	92	7.81	1.30	74
Resting total	80.49	2.21	84	71.24	3.15	131	55.51	2.22	126
Rub				0.26	0.05	2	1.35	0.39	22
Stroke partial									
Stroke complete				0.67	0.26	11	4.58	0.76	43
Stroke total				0.67	0.26	11	4.58	0.76	43
Lick	1.45	0.08	3	3.06	0.41	17	2.62	0.42	24
Lateral roll partial				0.04	0.10	4	0.30	0.16	9
Lateral roll complete				0.17	0.05	2	0.43	0.21	12
Lateral roll total				0.20	0.14	6	0.73	0.37	21
Shoulder roll partial				0.01	0.02	1	0.05	0.02	1
Shoulder roll complete				0.35	0.22	9	0.05	0.05	3
Shoulder roll total				0.36	0.24	10	0.09	0.07	4
Forward roll partial*							0.01	0.02	1
Forward roll complete*									
Forward roll total*							0.01	0.02	1
Headshake		0.03	1		0.55	23		0.37	21
Hang*				0.002	0.02	1	1.50	0.44	25
Bubble							0.05	0.02	1
Travel dorsal				0.11	0.07	3	0.06	0.04	2
Travel ventral	0.02	0.03	1	0.57	0.14	6	4.49	1.44	82
Nurse	7.09	0.16	6	10.11	0.29	12	7.69	0.30	17
Periscope									
Dive foraging							0.78	0.25	14
Dive non-foraging							0.36	0.28	16
Dive total							1.14	0.53	30
Mani. food w/consumption							1.96	0.35	20
Mani. food w/o consumption	0.11	0.05	2	0.07	0.02	1	1.01	0.23	13
Chest pound partial									
Chest pound complete							0.01	0.04	2
Chest pound total							0.01	0.04	2
Take food from mother									
Mother gives food to pup								0.51	29
Environmental exploration	0.03	0.03	1	0.18	0.07	3	3.23	0.42	24
Misc. active behaviors*	12.25	0.61	23	11.25	1.39	58	14.80	3.15	179

* Not presented in graphs

Appendix 2, continued.

Age in weeks	7-8			9-10			11-12		
	%	fr	n	%	fr	n	%	fr	n
Resting quiet	43.04	0.85	34	39.73	0.94	51	19.05	0.66	15
Resting alert	6.47	1.38	55	5.54	1.46	79	0.82	0.71	16
Resting total	49.51	2.23	89	45.27	2.39	130	19.87	1.37	31
Rub	1.10	0.25	10	2.57	0.74	40	3.73	1.06	24
Stroke partial							0.04	0.04	1
Stroke complete	3.78	0.90	36	4.52	1.05	57	6.65	2.69	61
Stroke total	3.78	0.90	36	4.52	1.05	57	6.69	2.73	62
Lick	0.97	0.30	12	2.76	0.44	24	4.36	1.63	37
Lateral roll partial	0.53	0.15	6	0.19	0.18	10	0.02	0.13	3
Lateral roll complete	0.12	0.20	8	0.73	0.52	28	1.53	0.97	22
Lateral roll total	0.65	0.35	14	0.91	0.70	38	1.58	1.10	25
Shoulder roll partial	0.06	0.18	7						
Shoulder roll complete	0.02	0.08	3	0.50	0.39	21	1.00	0.66	15
Shoulder roll total	0.07	0.25	10	0.50	0.39	21	1.00	0.66	15
Forward roll partial*									
Forward roll complete*				0.01	0.04	2	0.26	0.22	5
Forward roll total*				0.01	0.04	2	0.26	0.22	5
Headshake		0.48	19		0.72	39		1.50	34
Hang*	0.10	0.28	11	0.13	0.11	6			
Bubble	0.25	0.03	1	0.17	0.07	4	0.04	0.09	2
Travel dorsal	0.37	0.08	3	0.74	0.35	19	3.19	1.15	26
Travel ventral	3.92	1.45	58	7.17	2.36	128	7.56	4.11	93
Nurse	22.66	0.58	23	11.92	0.44	24	10.97	0.93	21
Periscope		0.02	1		0.13	7		0.53	12
Dive foraging	3.00	0.95	38	2.64	0.79	43	10.68	4.02	91
Dive non-foraging	0.38	0.33	13	0.25	0.07	4	0.48	0.66	15
Dive total	3.38	1.28	51	2.89	0.87	47	11.16	4.68	106
Mani. food w/consumption	2.82	0.68	27	5.81	0.79	43	17.03	4.64	105
Mani. food w/o consumption	0.28	0.10	4	6.57	0.48	26	1.46	0.62	14
Chest pound partial	0.04	0.08	3	0.05	0.15	8	0.16	0.57	13
Chest pound complete	0.005	0.02	1	0.02	0.06	3	0.03	0.04	1
Chest pound total	0.05	0.10	4	0.07	0.20	11	0.19	0.62	14
Take food from mother		0.20	8		0.39	21		0.80	18
Mother gives food to pup		0.53	21		0.39	21		1.90	43
Environmental exploration	0.86	0.23	9	0.61	0.18	10	2.10	0.31	7
Misc. active behaviors*	11.63	2.78	111	11.57	3.48	189	8.76	6.49	147

* Not presented in graphs

Appendix 2, continued.

Age in weeks	13-14			15-20			21-26		
	%	fr	n	%	fr	n	%	fr	n
Resting quiet	61.12	0.55	22	10.62	0.41	16	41.20	0.70	20
Resting alert	7.53	0.92	37	2.73	1.63	64	1.71	1.12	32
Resting total	68.65	1.47	59	13.35	2.03	80	42.91	1.83	52
Rub	3.45	0.47	19	3.52	1.40	55	4.94	1.40	40
Stroke partial									
Stroke complete	6.68	0.82	33	4.56	1.68	66	6.65	2.63	75
Stroke total	6.68	0.82	33	4.56	1.68	66	6.65	2.63	75
Lick	7.03	0.62	25	3.82	1.22	48	3.58	0.70	20
Lateral roll partial							0.83	0.14	4
Lateral roll complete	1.06	0.57	23	1.48	1.37	54	0.73	0.88	25
Lateral roll total	1.06	0.57	23	1.48	1.37	54	1.52	1.02	29
Shoulder roll partial	0.99	0.07	3				0.66	0.14	4
Shoulder roll complete	2.92	0.87	35	0.67	1.17	46	0.19	0.25	7
Shoulder roll total	3.91	0.95	38	0.67	1.17	46	0.85	0.39	11
Forward roll partial*									
Forward roll complete*	0.02	0.05	2	0.03	0.13	5	0.02	0.04	1
Forward roll total*	0.02	0.05	2	0.03	0.13	5	0.02	0.04	1
Headshake		0.10	4		0.81	32		0.67	19
Hang*	0.07	0.05	2	0.19	0.38	15	0.07	0.07	2
Bubble	0.07	0.05	2	0.26	0.36	14	0.57	0.32	9
Travel dorsal	0.08	0.07	3	3.72	1.60	63	3.09	1.05	30
Travel ventral	2.78	0.90	36	8.06	4.80	189	1.51	0.91	26
Nurse	9.30	0.37	15	20.21	1.12	44	26.13	0.95	27
Periscope		0.15	6		3.94	155		0.60	17
Dive foraging	0.85	0.17	7	19.78	6.53	257	5.25	1.48	42
Dive non-foraging	0.01	0.02	1	0.91	1.04	41	0.31	0.25	7
Dive total	0.86	0.20	8	20.69	7.57	298	5.56	1.72	49
Mani. food w/consumption	1.70	0.50	20	11.40	5.26	207	4.07	1.58	45
Mani. food w/o consumption	0.08	0.07	3	2.22	0.99	39	0.63	0.07	2
Chest pound partial				0.73	0.71	28	0.11	0.18	5
Chest pound complete	0.02	0.02	1	0.13	0.20	8	0.01	0.04	1
Chest pound total	0.02	0.02	1	0.86	0.91	36	0.11	0.21	6
Take food from mother		0.40	16		2.62	103		0.95	27
Mother gives food to pup		0.12	5		0.89	35		0.18	5
Environmental exploration				0.50	0.23	9			
Misc. active behaviors*	4.08	1.52	61	11.41	9.52	375	6.39	3.72	106

* Not presented in graphs

Appendix 3. Mean bout length (x), standard deviation (s.d.), and sample size (n) for each pup behavior for each age interval.

Age in weeks	1-2			3-4			5-6		
	$\bar{x}$	s.d.	n	$\bar{x}$	s.d.	n	$\bar{x}$	s.d.	n
Resting quiet	572.11	801.91	37	601.36	714.01	33	299.32	1143.72	43
Resting alert	75.82	93.61	40	53.04	67.13	90	55.69	108.12	72
Resting total	314.30	609.42	77	200.15	443.30	123	223.05	957.74	115
Rub				54.50	17.68	2	35.48	34.92	22
Stroke				25.45	28.20	11	60.58	76.78	43
Lick	183.33	67.42	3	78.20	72.26	15	62.08	88.70	24
Lateral roll partial				4.00	4.00	4	20.75	20.72	8
Lateral roll complete				34.50	27.58	2	19.00	20.25	13
Lateral roll total				14.17	20.24	6	19.67	19.93	21
Shoulder roll partial				5.00	0.00	1	27.00	0.00	1
Shoulder roll complete				16.00	10.42	9	9.00	13.86	3
Shoulder roll total				14.90	10.42	10	13.50	14.46	4
Forward roll partial*							4.00	0.00	1
Forward roll complete*									
Forward roll total*							4.00	0.00	1
Hang*				1.00	0.00	1	34.16	28.44	25
Bubble							27.00	0.00	1
Groom mother	4.00	0.00	2	51.33	63.44	3	30.00	31.76	4
Play with mother	29.92	46.57	4	105.00	100.25	7	38.20	20.00	20
Travel dorsal							16.50	4.95	3
Travel ventral	7.00	0.00	1	39.67	51.74	6	31.05	35.47	80
Nurse	448.50	430.94	6	371.88	260.97	8	155.71	192.69	14
Dive foraging							31.79	15.72	14
Dive non-foraging							12.62	11.64	16
Dive total							21.57	16.60	30
Mani. food w/consumption							57.21	51.75	19
Mani. food w/o consumption	20.50	3.54	2	30.00	0.00	1	44.38	42.43	13
Chest pound partial									
Chest pound complete							2.50	0.71	2
Chest pound total							2.50	0.71	2
Environmental exploration	12.00	0.00	1	17.08	12.60	3	112.00	144.79	14
Misc. active behaviors*	176.04	224.97	22	109.26	173.44	49	44.97	92.59	177

* Not presented in graphs

Appendix 3, continued

Age in weeks	7-8			9-10			11-12		
	$\bar{x}$	s.d.	n	$\bar{x}$	s.d.	n	$\bar{x}$	s.d.	n
Resting quiet	314.03	479.07	29	174.38	310.15	37	214.38	513.49	13
Resting alert	46.09	53.05	54	35.73	81.00	74	11.56	8.35	16
Resting total	139.71	310.98	83	81.95	200.37	111	102.48	351.54	29
Rub	43.80	61.25	10	35.64	43.13	39	29.22	33.42	23
Stroke	41.94	91.11	36	43.05	60.01	55	24.12	33.72	59
Lick	32.42	42.18	12	62.42	93.03	24	26.65	29.06	37
Lateral roll partial	35.17	47.27	6	5.75	3.77	4			
Lateral roll complete	6.00	4.72	8	13.08	27.64	38	13.42	24.65	24
Lateral roll total	18.50	33.10	14	12.37	26.34	42	13.42	24.65	24
Shoulder roll partial									
Shoulder roll complete	2.00	0.00	1	14.96	20.77	23	15.07	28.08	15
Shoulder roll total	2.00	0.00	1	14.96	20.77	23	15.07	28.08	15
Forward roll partial*									
Forward roll complete*				3.50	0.71	2	11.60	14.98	5
Forward roll total*				3.50	0.71	2	11.60	14.98	5
Hang*	3.2	3.70	12	12.17	14.02	6			
Bubble	100.00	0.00	1	23.00	28.86	4	4.00	2.83	2
Groom mother	11.00	0.00	1	230.00	0.00	1			
Play with mother	7.50	3.54	2	28.50	30.26	4	18.25	15.90	4
Travel dorsal	37.25	4.79	4	21.00	25.48	19	25.67	47.62	21
Travel ventral	26.46	38.86	56	28.10	39.76	11	18.18	20.01	89
Nurse	338.95	484.92	20	233.11	490.62	19	73.60	111.62	20
Dive foraging	30.82	17.31	39	32.36	16.09	44	26.48	21.94	92
Dive non-foraging	12.33	16.65	12	41.00	56.57	2	20.90	31.33	14
Dive total	26.47	18.74	51	32.74	17.93	46	23.83	21.61	106
Mani. food w/consumption	41.70	45.33	27	73.97	80.57	39	37.75	49.12	88
Mani. food w/o consumption	27.75	17.46	4	137.12	320.28	26	23.64	18.36	14
Chest pound partial				3.75	3.65	8	2.77	2.92	13
Chest pound complete	4.75	2.22	4	1.75	0.50	4	7.00	0.00	1
Chest pound total	4.75	2.22	4	3.08	3.09	12	3.07	3.02	14
Environmental exploration	43.33	38.21	3	11.50	4.51	4	75.33	63.51	6
Misc. active behaviors*	41.81	73.90	115	29.75	46.54	16	11.39	29.78	135

* Not presented in graphs

Appendix 3, continued.

Age in weeks	13-14			15-20			21-26		
	$\bar{x}$	s.d.	n	$\bar{x}$	s.d.	n	$\bar{x}$	s.d.	n
Resting quiet	1128.27	1773.09	15	307.70	309.00	8	476.06	709.43	16
Resting alert	82.36	246.87	36	16.43	33.19	68	15.19	13.34	32
Resting total	389.98	1074.52	51	47.09	134.15	76	168.81	457.11	48
Rub	69.39	101.83	18	25.16	74.40	55	35.18	68.58	40
Stroke	79.00	132.87	30	24.42	34.50	66	25.24	34.00	75
Lick	110.18	130.13	22	31.33	47.30	48	50.90	62.46	20
Lateral roll partial							59.00	76.41	4
Lateral roll complete	12.80	15.10	20	9.83	14.44	52	8.32	10.21	25
Lateral roll total	12.80	15.10	20	9.83	14.44	52	15.31	32.11	29
Shoulder roll partial	133.00	153.48	3				47.25	52.68	4
Shoulder roll complete	26.88	29.20	33	5.72	10.96	46	7.57	4.86	7
Shoulder roll total	35.72	54.87	36	5.72	10.96	46	22.00	35.32	11
Forward roll partial*									
Forward roll complete*	5.00	2.83	2	5.39	10.46	5	7.00	0.00	1
Forward roll total*	5.00	2.83	2	5.39	10.46	5	7.00	0.00	1
Hang*	10.00	0.00	1	4.87	3.85	15	9.50	4.95	2
Bubble	15.00	7.07	2	6.69	7.08	13	18.11	19.15	9
Groom mother	57.67	51.29	3	5.28	4.96	7	13.38	14.08	8
Play with mother	17.00	19.08	3	34.60	26.09	5	12.75	13.21	8
Travel dorsal	11.00	14.73	3	20.39	33.32	57	29.37	50.77	30
Travel ventral	31.65	45.17	34	15.61	28.73	179	17.46	16.87	24
Nurse	248.67	373.64	15	171.78	275.87	41	257.75	289.86	24
Dive foraging	43.43	20.46	7	30.28	25.77	255	35.62	27.80	42
Dive non-foraging				9.44	9.51	41	12.43	10.20	7
Dive total	43.43	20.46	7	27.39	25.22	296	32.31	27.21	51
Mani. food w/consumption	36.00	24.00	17	21.03	20.37	196	22.52	27.16	42
Mani. food w/o consumption	11.00	4.24	2	22.44	17.82	39	89.00	104.65	2
Chest pound partial				7.78	7.05	23	3.67	3.06	3
Chest pound complete	9.00	0.00	1	12.38	16.11	13	7.00	7.81	3
Chest pound total				9.44	11.19	36	5.33	5.61	6
Environmental exploration				21.78	10.44	9			
Misc. active behaviors	26.77	70.26	56	11.87	20.31	353	17.10	40.91	96

* Not presented in graphs