

Weaning in an arctic wolf pack: behavioral mechanisms

J. M. PACKARD

Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843-2258, U.S.A.

L. D. MECH

U.S. Fish and Wildlife Service, North Central Forest Experiment Station, 1992 Folwell Avenue, St. Paul, MN 55108, U.S.A.

AND

R. R. REAM

School of Forestry, University of Montana, Missoula, MT 59812, U.S.A.

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If behavioral mechanisms controlling suckling have been shaped by parent–offspring conflict in the ultimate sense, then proximate behavioral determinants of conflict should occur throughout lactation, with greatest intensity in the terminal phase, and offspring should have tactics for overcoming parental resistance. We observed the weaning process in a habituated wild wolf pack (*Canis lupus*) on Ellesmere Island, Canada, from estimated ages 5 through 10 weeks (including a continuous record for 192 h). The following variables declined with age: percentage of suckling bouts initiated by the nurser, persistence by pups, and mean duration of suckling bouts. Variables that increased with age were interbout interval, percentage of suckling bouts terminated by the nurser, and wincing or agonistic actions of the nurser. Behavioral conflict appeared in the developmental stage (estimated age 7–8 weeks) during which pups could feed on opened carcasses. Countertactics by pups to obtain milk were not apparent, although the pups developed diverse tactics for obtaining and sharing meat. In this group of wolves, weaning mechanisms were a complex function of food delivery by adults, discomfort of the nursing female as pups developed, and declining persistence of pups. If there is a conflict over what is optimal for pups and for the nurser in the ultimate sense, behavioral conflict is more likely to be expressed with regard to access to meat, or as conditional tactics dependent on food availability, rather than weaning conflict being controlled by fixed rules in this species.

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Si l'on admet que les mécanismes comportementaux qui régissent l'allaitement ont comme causes ultimes des conflits parents–progéniture, il est normal de penser que des facteurs comportementaux proximaux interviennent durant toute la période de lactation, avec une intensité maximale durant la phase terminale, et que les petits ont des tactiques pour venir à bout de la résistance parentale. Nous avons observé le processus de sevrage chez une meute de Loups gris (*Canis lupus*) acclimatés dans l'île Ellesmere, Canada, entre les âges de 5 et 10 semaines environ (y compris pendant une période continue de 192 h). Les variables suivantes diminuent avec l'âge : le pourcentage de périodes d'allaitement provoquées par le loup nourricier, la persistance des louveteaux, la durée moyenne des périodes d'allaitement. Les variables suivantes augmentent en fonction de l'âge : les intervalles entre les périodes d'allaitement, le pourcentage de périodes d'allaitement terminées par le loup nourricier, les mouvements d'impatience et les réactions agonistiques des loups nourriciers. Les conflits apparaissent au cours du développement (vers l'âge de 7–8 semaines) lorsque les louveteaux peuvent se nourrir de carcasses ouvertes. Les petits ne semblent pas utiliser de contrestratégies pour obtenir du lait, mais ils se servent de diverses tactiques pour obtenir de la viande et la partager. Chez ce groupe de loups, les mécanismes du sevrage sont donc constitués d'un complexe de facteurs, notamment l'apport de nourriture par les adultes, l'inconfort ressenti par la femelle nourricière à mesure que les petits vieillissent et la persistance de moins en moins grande des louveteaux. S'il existe un conflit entre les conditions optimales pour les petits et les conditions optimales pour le loup nourricier au sens ultime, le conflit comportemental risque de se manifester plutôt par rapport à l'accès à de la viande, ou sous forme de tactiques conditionnelles adaptées à la disponibilité de la nourriture, plutôt que comme règles strictes contrôlant le conflit entourant le sevrage chez cette espèce.

[Traduit par la rédaction]

Introduction

Theoretically, under certain environmental conditions infants would have evolved to demand more than nursing mothers were designed to give (Trivers 1974). Behavioral conflict during suckling bouts has been interpreted as evidence for this underlying conflict resulting from disparate ultimate determinants of behavioral mechanisms controlling contests over milk transfer (Trivers 1974). However, species differ in the extent to which nursers and infants play an active role in the weaning process (Babbitt and Packard 1990a) and the degree to which suckling effort is directly related to milk transfer (Mendl and Paul 1989). Furthermore, environmental factors such as diet (Babbitt and Packard 1990b) can influence the expression of behavioral conflict during weaning.

The following predictions were made for species that have evolved under conditions in which the ultimate determinants of infants' suckling behavior have produced mechanisms different from those that are optimal for the nurser. Throughout lactation, offspring should demand more than the nurser is willing to give, meaning that the nurser interrupts suckling more frequently than the infants do (Trivers 1974). The intensity of conflict should increase in the intermediate (Martin 1984) or terminal (Trivers 1974) phase of lactation, resulting in weaning when the costs to the nurser reach a threshold that would affect future reproduction. In the terminal phase, the infant should persist in obtaining more parental care when the nurser interrupts suckling attempts, even though such countertactics may be costly (Stamps et al. 1985).

Although several studies have examined developmental changes in suckling behavior (Hall and Williams 1983), few have focused on the behavioral processes resulting in the loss of suckling behavior from the repertoire of infants (Chalmers 1987). Furthermore, with the exception of Martin's (1986) study of weaning in house cats, there is little information on weaning in carnivores. Developmental studies of canids generally have not focused on suckling (Bekoff 1978; Knight 1978; Frame 1985; Havkin and Fentress 1985; MacDonald 1987). In addition, canid dens in forested habitat are very difficult to observe, requiring the use of remote monitoring techniques (Harrington and Mech 1978).

The weaning process in wolves may be readily observed in tundra habitat, where continuous daylight permits observation at all hours of the day (Murie 1944). When wolf pups emerge from the den, they generally remain in the area of the den or a nearby "rendezvous site" (Murie 1944; Mech 1970). Pack members return to feed the pups, and suckling occurs outside the den. However, previous observations of tundra wolves have been from a long distance.

We observed the weaning process in a habituated wild pack of wolves in the Canadian Arctic (Ellesmere Island), and analyzed the data to test the predictions outlined above. The purpose of the analysis was to determine if maternal conflict occurred throughout lactation and was more intense at the time of weaning, and whether infants had tactics countering the nurser's actions. We define weaning as the spontaneous cessation of suckling behavior by the infant, in contrast to other definitions discussed by Martin (1984).

Methods

Subjects

The pack of four adult wolves had been habituated to the presence of observers during the previous two summers (Mech 1988). The adults included the nursing female, a dominant male, a nonlactating submissive female, and a submissive male. The sex and status of each wolf was determined by the characteristic urination posture (Peters and Mech 1975). Based on identifying features and behavior, we determined that the nursing female was the same as in the previous year; however, the dominant males were different in the 2 years. The submissive female was probably at least 2 years old and the submissive male was a yearling. A fifth yearling-like wolf approached the pack once but was not otherwise seen near the den and pups. An unidentified wolf was observed with pack members at a garbage dump 3 km from the den.

Four pups emerged from the den 1 week prior to the beginning of observations (J. Brandenburg, personal communication). We estimated the age of the pups to be 5–10 weeks during this study (22 June – 1 August 1988). The eyes of wolf and dog pups open at about 2 weeks (Scott and Fuller 1965), and wolf pups can maneuver over obstacles at that age (Zimen 1971). Emergence from the den is likely to be in the third week. Judging from urination postures observed simultaneously, the litter included three males and one female. Individual identities of pups could not be determined reliably.

Data collection

The pups were observed for as long as possible (6–24 h) during each calendar day from a distance of 10–500 m, with the aid of binoculars (15 × 60). The procedure was to record all occurrences of suckling and feeding bouts.

During the first few weeks the pups were at a rendezvous site distant from the den, and two observation stations were needed to view the entire area, which included a ridge and part of a valley that could not be viewed from one station. To obtain a complete record during 8- to 12-h samples, one observer (J.M.P. or L.D.M.) was stationed on each side of the ridge or valley at the rendezvous site.

Observation sessions were distributed across all hours of the 24-h cycle. During the last 3 weeks of the study, the pups were visible from one viewing station; two observers (J.M.P. or R.R.R.) were able to maintain continuous 24-h observations by shifts. The week in which weaning occurred was included in a 192-h continuous record. Observations were also continuous in the final week of the study.

Data analysis

The variables we analyzed included duration of suckling bout, interbout interval, initiator of suckling bouts, terminator of suckling bouts, number of pups persisting after termination, and agonistic actions during suckling-bout termination. These variables are defined below.

The duration of a suckling bout was the number of minutes from suckling contact by the first pup until the last pup broke contact with the inguinal area of the nurser. Suckling attempts interrupted by less than 2 min were considered part of the bout. The interbout interval was the time (measured in hours) between two subsequent bouts.

Suckling bouts were categorized as being initiated by the pups or by the nurser. The nurser initiated a suckling bout by approaching and whining softly near the pups, which often were sleeping. Pups initiated a suckling bout by approaching the nurser, often when she returned from an absence, but occasionally when she was sleeping.

Suckling bouts were categorized as terminated by the nurser or by the pups. The nurser terminated a suckling bout by walking away or turning her rear away from the pups. If one or more pups broke contact with the nipples prior to the nurser moving away, the suckling bout was categorized as terminated by the pups. This categorical rule was justified because sometimes the nurser seemed to sense that the pups were finished. For example, when one or two pups left her belly and moved near her head, the nurser often looked back toward the pups, took a few tentative steps, then walked away if pups did not persist. In such cases, she did not appear to be stopping a suckling bout against the pups' interests, so the bout was categorized as terminated by the pups.

We measured persistence by pups as the number (0, 1 or 2, 3 or 4) following the nurser when she terminated a suckling bout. The following-response varied in intensity, from simply trotting along behind to active attempts to regain contact with the nipples. We interpreted following as indicating that pups were not finished suckling. Persistence has been shown to be a more sensitive variable than nurser interruptions in another species (Babbitt and Packard 1990b).

Suckling bouts were categorized by the presence or absence of agonistic actions during termination. The nurser showed two types of agonistic actions: "wincing" and "over-the-muzzle" biting of pups. Wincing was a quick, startled movement away from pups. In an over-the-muzzle bite, the jaws are closed firmly but without inflicting injury (Zimen 1971). Often pups continued whatever activity elicited the over-the-muzzle bite, although the intensity of crouching and tail wagging often increased.

Categorical variables were analyzed using the χ^2 test. The contingency matrices contained the frequencies of bouts in each category for each week (estimated ages 5–9 weeks). To determine which cells of the contingency tables contributed significantly to the χ^2 , Freeman–Tukey deviates (Bishop et al. 1975) were calculated.

The effect of estimated age on bout duration and interbout interval was determined using analysis of variance. The variation within each week was used as the error term to test the significance of the variation between weeks. Sample sizes ranged from 9 to 26 per week for bout duration and from 3 to 21 per week for interbout interval. Although these samples were unevenly distributed across weeks, the test used was robust in accounting for such variation from an evenly blocked experimental design.

Results

Suckling-bout duration and interval

Usually all pups suckled simultaneously with the nurser in a standing position. Mean bout duration declined steadily with age, and mean interbout interval increased substantially

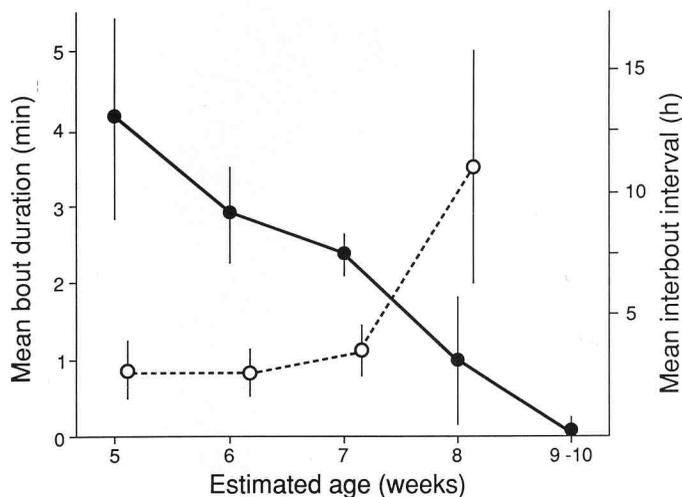


FIG. 1. Changes in mean duration (●) and intervals (○) between suckling bouts relative to estimated age of pups in the Ellesmere wolf pack. Vertical lines show 95% confidence intervals.

between weeks 7 and 8 (Fig. 1). The effect of age on interbout interval was highly significant ($F = 11.24$; $p < 0.001$; SS between = 2.66×10^6 , $df = 4$; SS within = 4.102×10^6 , $df = 56$), as was the effect on bout duration ($F = 7.15$; $p < 0.001$; SS between = 3.556×10^5 , $df = 4$; SS within = 8.947×10^5 , $df = 76$).

Bouts were 3–5 min long when pups were young. Mean bout duration declined steadily to less than 1 min at age 9–10 weeks. The variance in bout duration was higher in week 8 than in weeks 6, 7, and 9, suggesting a transition phase. The chronology of events (Fig. 2) illustrates that successful bouts in week 8 lasted the typical 3 min. Mean bout duration declined because there were many short bouts (unsuccessful) in this period of transition, rather than progressively more bouts of intermediate length.

Interbout intervals were less than 5 h during weeks 5–7, increasing abruptly to over 15 h in week 8. Variance in interbout intervals was also highest in week 8. We were unable to record interbout intervals in week 9, owing to the low frequency.

Suckling-bout initiation and persistence

The percentage of suckling bouts initiated by the nurser and persistence by the pups declined with age (Fig. 3). A transition appeared in week 8.

The nurser initiated most bouts in week 6, declining gradually to none in week 10. The relative frequency of bouts initiated by the nurser or pups changed significantly with age ($\chi^2 = 19.36$, $df = 4$, $p < 0.001$). Bouts were initiated by the nurser more frequently than expected in weeks 6–7 (Freeman–Tukey deviate > 1) and by the pups more frequently than expected for weeks 9–10 (Freeman–Tukey deviate > 1). In week 10, single pups initiated suckling attempts rather than the whole litter as was typical of weeks 6–9 (Fig. 2).

Most of the litter (3 or 4 pups) persisted in attempting to suckle after the bout was terminated during weeks 6–7. However, persistence was low in weeks 8–10. The relative frequency of bouts in which none, half (1 or 2 pups), or most (3 or 4 pups) of the litter persisted differed significantly with age ($\chi^2 = 28.02$, $df = 8$, $p < 0.001$). During week 8 (Fig. 2), more pups persisted after successful, long bouts than after unsuccessful, short bouts.

Termination of bouts

The percentage of bouts terminated by the nurser increased steadily from 25 to 100 in week 9 (Fig. 4). The relative frequency of bouts terminated by the nurser or pups differed significantly with age ($\chi^2 = 14.94$, $df = 4$, $p < 0.005$). The nurser terminated fewer bouts than expected in week 5 (Freeman–Tukey deviate < -1) and more bouts than expected in weeks 8 and 9 (Freeman–Tukey deviate > 1).

Only once did an agonistic interaction terminate suckling prior to week 7. During weeks 7–8, the nurser winced four times and muzzled the pups three times. In the last 2 weeks, the nurser winced once and muzzled the pups four times. On the occasions when the nurser winced or muzzled the pups, the pups did not persist (Fig. 2). The frequency of agonistic actions was too low for statistical tests to be run.

Discussion

The data did not support our predictions. On the contrary, conflict was not apparent throughout lactation, and counter-tactics for overcoming nurser rejection did not occur. Consistent with predictions, however, nurser interruptions did increase with age and agonistic interactions were most intense in the last week during which suckling was observed. However, wincing and muzzling by the nurser were inconsistent and infrequent and appeared to be a response to discomfort caused by the pups' teeth, rather than an indication of parent–offspring conflict in the ultimate sense. The reasons for this interpretation are described more fully below.

When predictions based on a model are rejected, several possibilities must be considered prior to rejecting the model: (i) the assumptions of the model were not met, (ii) the variables measured were not directly related to the factors defined in the model, or (iii) the sample was biased or inadequate. These possibilities are considered in the following discussion.

Conflict throughout lactation

Trivers (1974) predicted that if offspring consistently demand more than the parent can give, conflict would be apparent in each suckling bout. A suckling bout may be viewed as a contest over resources (Hauser 1986), and the more resources a nurser loses, the more likely she will suffer a reduction or delay in the subsequent litter. However, as argued by Galef (1983), not all effort expended in reproduction results in ultimate costs.

In the present study, the nurser did not consistently stop suckling bouts. At age 5 weeks, no conflict was apparent in the interaction between the pups and nurser, when the nurser initiated 92% and only terminated 25% of the suckling bouts. If there was a latent conflict not overtly expressed, we would have expected persistence to increase; however, we observed a decline. Therefore we would not interpret the high persistence in week 5 as evidence for latent conflict, but rather as evidence of a developmental stage in which following was important, possibly for other reasons such as pack cohesion and safety of pups when they are moved between den sites.

We conclude that conflict during suckling does not always occur throughout the period of lactation in wolves. The degree to which this conclusion is situation or species specific remains to be determined. For example, if the tactics vary according to the nutritional condition of the nurser or infant (Bateson 1981; Babbitt and Packard 1990a), then conflict over suckling might be expected to occur when food quality or availability is low. Obviously we cannot claim that the pattern documented

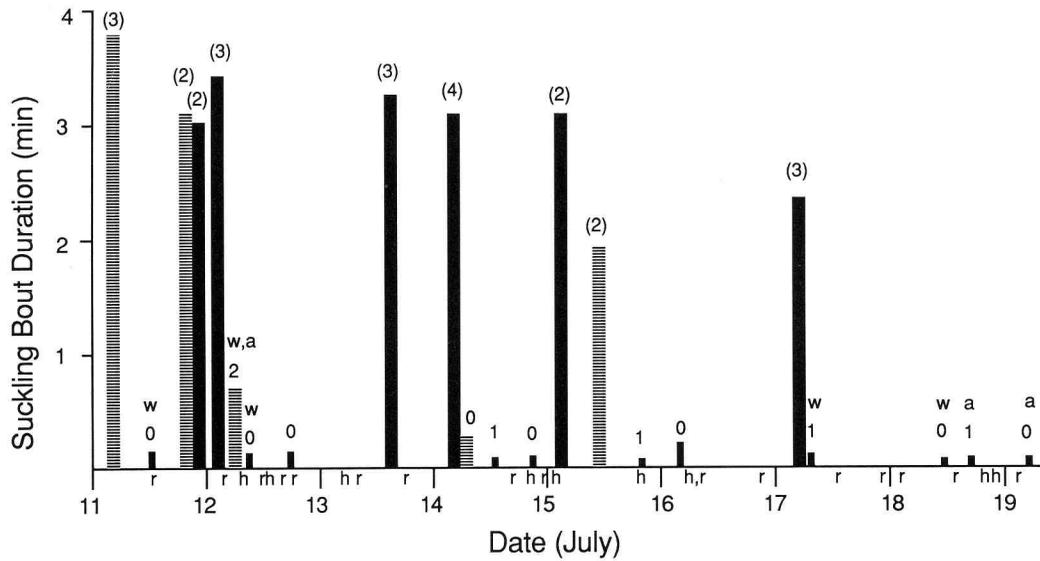


FIG. 2. Chronology of weaning bouts when pups in the Ellesmere wolf pack were estimated to be 8–9 weeks of age. Vertical bars represent the duration of each bout terminated by one or more pups (hatched bars) or the female (solid bars). Narrow bars indicate suckling bouts initiated by only 1 or 2 pups. Numbers in parentheses are the number of pups persisting after termination of long (successful) bouts. Behavior is indicated as follows: *h*, delivery of hare carcasses; *r*, regurgitations; *w*, wincing by the nurser; *m*, muzzling by the nurser.

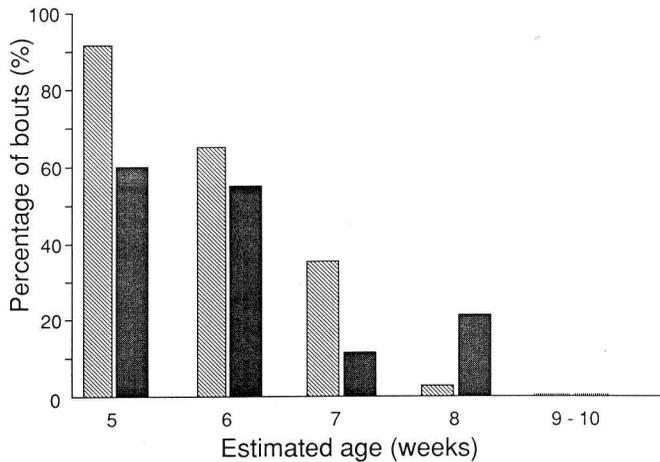


FIG. 3. Percentage of bouts initiated by the nurser (hatched bars) and percentage of bouts with 3 or 4 pups persisting (shaded bars) relative to the estimated age of pups in the Ellesmere wolf pack.

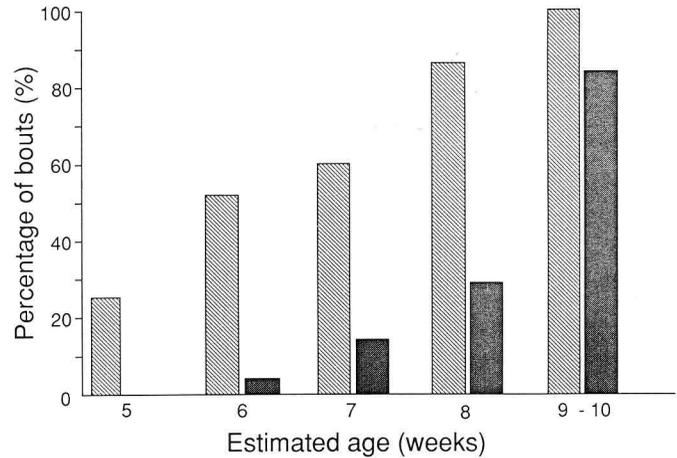


FIG. 4. Percentage of bouts terminated by the nurser (hatched bars) and percentage of bouts involving agonistic actions by the nurser (shaded bars) relative to estimated age of pups in the Ellesmere wolf pack.

in this one study is characteristic of the species as a whole. However, we can reject the null hypothesis that conflict always occurs throughout lactation.

The assumptions of Trivers' (1974) optimality model include a stable environment and a direct relationship between parental care (nursing behavior) and parental investment (anything that reduces future reproductive effort). Both of these assumptions are unlikely to be true for long-lived mammals. Food availability can vary substantially from year to year within the lifetime of one wolf, depending on changes in prey availability and weather (Packard and Mech 1980).

In addition, wolves are seasonal breeders, ovulating in February–March (Seal et al. 1987), so nursers have many months to restore body condition after weaning. Babbitt and Packard (1990a, 1990b) rejected several predictions based on the optimality model of Trivers (1974) after examining data

from another species adapted to a fluctuating environment, the collared peccary (*Tayassu tajacu*). They argued that for seasonally reproducing mammals, there may be enough time for a female to recover energy reserves, so there might not be expected to be a direct relation between milk transfer and parental investment, e.g., the last ounce of milk may not lower a female's body condition below a threshold that influences ovulation 6–8 months later.

Therefore, our observations that conflict does not always occur throughout lactation in wolves are not sufficient to reject the optimality model of Trivers (1974). These results underscore the need for a model designed to address ultimate factors affecting the behavior of species adapted to a fluctuating environment. Rubenstein (1982) addressed the importance of looking at the variance as well as the average payoffs of alter-

TABLE 1. Developmental stages of the pups from 5 to 10 weeks of age in the Ellesmere wolf pack

Age (weeks)	Suckling	Regurgitation	Feeding	Play/social
5	Nursing initiated	None	Chewing difficult	Uncoordinated; paw on back; mouth and roll
6	Following frequent at end of bout	Infrequent	Ate opened carcasses	More mobile; stalk and pounce; dig; stand over
7	Pups did not always start suckling when nurser approached	Frequent active begging	Same	Intense and prolonged wrestle and chase; subtle aggression
8	Nursing winced	Very frequent	Defended carcass	Short independent trips
9	Only single pups	Same	Could open carcass	Play bouts lasting 1 h; muzzled by adults
10	None	Same	Same	Followed adults while hunting

native strategies, but did not extend his discussion to weaning conflict. Bull (1985) suggested that the inclusion of environmental variability in models of parent-offspring conflict can sometimes swamp the adaptive value of conflict, but also did not address the special case of weaning conflict.

Increasing conflict with age

Since the parent's cost/benefit ratio (expressed in terms of parental investment) increases over time, Trivers (1974) predicted that the intensity of weaning conflict would increase with age of the offspring. However, this trend would also be predicted by the alternative model that conflict is a function of developmental changes optimal for both the offspring and the parent. If the developmental model can be rejected for a particular species, then the parent-offspring conflict model would be more plausible.

Although data from the Ellesmere wolf pack indicate a trend toward increasing agonistic actions with age, we argue that such actions were not an expression of ultimate determinants of parent-offspring conflict. The agonistic actions appeared to be a function of physical and behavioral development of the pups (Table 1), as follows.

In week 5, the pups were relatively uncoordinated. They could barely lift a paw onto the back of a sib, and mouthed small meat chunks a long time before swallowing. Carcasses (arctic hare, *Lepus timidus*) brought to the area of the pups were eaten most frequently by the nurser and no regurgitations were recorded. In this week of dependence on milk, the nurser initiated most bouts and the pups terminated most bouts without conflict.

By week 6, the pups added "stalk and pounce," "digging," and "stand over" to their behavioral repertoire. They readily ate hare carcasses opened by adults and received infrequent regurgitations. The pups followed adults that carried pieces of meat and traveled with the nurser to new locations when she terminated a suckling bout. Following seemed to have a more important function in learning pack movements than in gaining access to the nurser because it occurred after suckling and did not terminate in a suckling bout. For example, pups followed the nurser to a meadow near the den and all adults in the pack were very preoccupied with the pups until the pups followed them back to a shelter site. Greater mobility of the pups at this stage may have led to more frequent initiation of bouts by pups. Pups were still primarily dependent on milk for nutrition

and still persisted in following when the nurser terminated a bout.

Noticeable developmental changes occurred in week 7, at the time Scott and Fuller (1965) mentioned that weaning occurs in dogs and wolves. Pups engaged in prolonged chasing and wrestling bouts with an intense, directed quality of movement. They actively begged ("lick up to the muzzle") and received frequent regurgitations from all pack members. Adult males disciplined pups with "over the muzzle" bites when they were overly active at begging; pups learned to stop leaping, and squirmed with bellies close to the ground. Pups no longer spontaneously initiated suckling when the nurser arose or returned and were markedly less persistent when bouts were terminated. The nurser seemed to distract pups with regurgitations at the end of a suckling bout. More frequent nurser interruptions occurred because attempts by only 1 or 2 pups rather than the entire litter were more frequent. Pups slept longer, cached meat frequently, and began to watch distant objects such as birds in this transition stage.

In week 8, the gang of pups started making short trips without adults, and play included subtle aggression, such as a lack of role reversal. The occasional aggression by the nurser appeared at a time when pups showed aggression toward each other and were capable of hurting adults. For example, one pup was able to monopolize an unopened hare carcass by slight lunges toward sibs. When the others went to the nurser and suckled, she winced and picked up the carcass, and the pups actively pulled on it. One pup even playfully muzzled the yearling male as he reclined. Another mouthed the yearling's side hard enough to make him wince. Adults delivered an average of 2 regurgitations and 1 hare per day, so pups were relatively independent of milk for nutritional needs. Pups persisted little after suckling interruptions.

By week 9, pups could tear apart unopened hare carcasses, and play bouts lasted about an hour. Only single pups attempted to suckle and did not persist when muzzled by the nurser. Pups squabbled more intensely over the hare carcasses, but usually all 4 fed from each carcass.

We interpret the wincing and muzzling actions of the nurser toward the pups as a response to physical discomfort, not necessarily indicative of an underlying genetic conflict. As described above, the agonistic actions of the nurser appeared at a developmental stage in which pups became very active, could feed on carcasses, and were learning how hard they

could bite and how much they could beg without eliciting aggression from adults. Other adults muzzled the pups at the same stage as the nurser.

Therefore, although agonistic interactions increased with age as predicted by Trivers (1974), detailed examination of the behavior suggested that conflict was not necessarily directly controlled by the mechanisms related to parental investment (maintenance of the nurser's body condition, hence the ability to produce the next litter). We interpret the increase in conflict to be related to development of the young, since conflict occurred in other contexts in addition to suckling at the same age. Another critical point is that the pups did not persist when muzzled, as would be expected if the ultimate determinants of their behavior had favored demanding more than the parent could give. Therefore we cannot reject the developmental model in favor of the model of parent-offspring conflict. The interests of the nurser and infants seemed to be in parallel rather than in conflict.

It is possible that parent-offspring conflict in wolves is expressed in contests over delivery of meat rather than milk. If this was the case, then the variables that we measured were not directly related to parental investment as defined in the model of parent-offspring conflict. Again, our results are not sufficient to allow the model to be rejected, but suggest that caution should be used in interpreting weaning conflict as being determined by ultimate factors of parental investment. We would interpret the increased wincing and muzzling of the nurser to be a response to the use of teeth by the pups, which would have been influenced by the ultimate advantages of individual skills at competing with other pups for solid food.

Costly countertactics

If there is a discrepancy in the age of weaning that is optimal for the nurser and for the infant, then the theory of parent-offspring conflict would predict that parents have tactics for weaning offspring earlier and offspring have tactics for countering such parental tactics (Stamps et al. 1985; Hauser 1986). Theoretically, if natural selection for countertactics is strong enough, such mechanisms may persist despite a potential cost in fitness of infants due to conflict.

We did not detect any countertactics by pups to obtain milk after a bout was terminated. Persistence declined rather than increased with age, the decline being pronounced at the developmental stage during which pups ate more meat and became more active. During this transition the agonistic actions of the nurser terminated bouts, and pups did not persist on such occasions, which suggests that the pups were "in agreement" with the nurser.

Pups were capable of persistence and sometimes of elaborate countertactics at the developmental stage during which weaning occurred. Such maneuvers occurred in the contexts of playing with sibs and adults, begging for regurgitation, and sharing carcasses. In the context of playing, begging, and sharing, pups did not leave when another wolf muzzled, snapped, or lunged. In contrast, the muzzling by the nurser in the context of suckling terminated the pups' attempts to gain access to nipples.

The nurser seemed to use subtle tactics to divert the pups' attention when they attempted to suckle. For example, she regurgitated or trotted over to a carcass and manipulated it in a way that attracted their interest. Her tactics worked; the pups did not counter or attempt to resume suckling.

The ultimate tactic for pups to use in countering early weaning by the nurser would be to disguise the presence of the teeth

and bite power that allowed them to feed on carcasses. However, the nurser winced at the same stage that pups began earnestly feeding on carcasses. Apparently, the pups were honest in providing information about their ability to use their teeth.

The argument might legitimately be raised that the one pack we observed did not represent the genotypic and phenotypic variation existing in the population. Perhaps this one litter of pups contained an unusually high proportion of individuals with the genetic basis for the variant "nonmanipulative altruists," or perhaps the nurser represented a rare variant that was unusually good at "mind reading." Krebs and Dawkins (1984) describe evolutionary processes by which the proportion of different variants of behavioral traits influencing communication may change in a population. For this reason, we do not claim to have tested Trivers' (1974) model or to have made a definitive statement on weaning processes in general for wolves. However, we do want to emphasize several subtle factors that need to be considered in interpreting field data on weaning.

Very few field studies of nondomestic species have yielded continuous records of the weaning process. Since wolf dens may be separated by as much as 20 km in the Canadian Arctic, it is extremely difficult to obtain a large sample from a given population in a given year. Year-to-year variation is high; for example, the pack we watched did not den at the same site, and role changes occurred in subsequent years (L. D. Mech, personal observation). If we exclude species adapted to a fluctuating environment from analysis of weaning processes, as would be required to test the optimization model of Trivers (1974), we might ignore behavioral diversity that would lead to formulation of more appropriate models.

For species adapted to a fluctuating environment and in which parental care consists of food delivery as well as lactation, the assumptions of the optimality model of weaning conflict are not met. Perhaps examination of parental care in terms of developmental "directing" and "stopping" rules (Chalmers 1987) would be more appropriate. However, even in a developmental conceptual framework, it is necessary to consider the environment as a player in addition to the nurser and infant.

Trivers (1974) made a significant contribution in arguing that the infant should be considered an active player as well as the nurser. We are now challenged to refine and elaborate testable models that include environmental variation, rather than indiscriminately using a difficult-to-test optimality model to explain all conflict during weaning.

Conclusions

Based on intensive, detailed observations of one pack of wild wolves, three predictions based on the theory of parent-offspring conflict were not supported. Conflict did not occur throughout lactation. Although conflict intensified with age, we could not reject the developmental model that such changes were synchronously advantageous for nurser and infants. Pups did not display countertactics for prolonging suckling bouts when interrupted by the nurser.

We interpreted the increase in agonistic actions by the nurser to be a function of the development of the pups unrelated to the benefits of obtaining milk. Suckling duration declined and interbout intervals increased at the developmental stage during which pups were capable of tearing hare carcasses. Two mechanisms probably were involved: the greater satisfaction of nutritional needs via regurgitated meat and car-

casses, and the developing likelihood of the pups causing discomfort to the nurser while suckling.

Our conclusions do not rule out the possibility that conflict in wolves may be more pronounced under ecological conditions in which the nutritional growth needs of the pups are not satisfied by solid food provided by adults. However, such conditional weaning processes (Bateson 1981) will be examined on a different theoretical basis from the genetically fixed strategies addressed by the optimality model of parent-offspring conflict.

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