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Abstract: Few studies of monogamous canids have addressed regurgitation in the context of extended parental care and alloparental care within family groups. We studied food transfer by regurgitation in a pack of wolves on Ellesmere Island, North West Territories, Canada, during 6 summers from 1988 through 1996. All adult wolves, including yearlings and a post-reproductive female, regurgitated food. Although individuals regurgitated up to five times per bout, the overall ratio of regurgitations per bout was 1.5. Pups were more likely to receive regurgitations (81%) than the breeding female (14%) or auxiliaries (6%). The breeding male regurgitated mostly to the breeding female and pups, and the breeding female regurgitated primarily to pups. The relative effort of the breeding female was correlated with litter size (Kendall's $\tau = 0.93$, $P = 0.01$).

Résumé : Peu d'études ont abordé la question de la régurgitation en relation avec les soins parentaux et alloparentaux au sein des familles chez les canidés monogames. Nous avons étudié le transfert de la nourriture par régurgitation au sein d'une meute de loups de l'île d'Ellesmere, Territoires du Nord-Ouest, Canada, durant six étés, de 1988 à la fin de 1996. Tous les loups adultes, y compris les jeunes de 1 an et les femelles post-parturientes, régurgitaient de la nourriture. Certains individus régurgitaient jusqu'à 5 fois par épisode, mais, dans l'ensemble, le nombre de régurgitations par épisode était de 1,5. Les petits étaient plus susceptibles de recevoir des régurgitations (81%) que les femelles reproductrices (14%) ou les auxiliaires (6%). Les mâles reproducteurs régurgitaient à leur partenaire et à leurs petits et les femelles reproductrices régurgitaient surtout à leurs petits. L'effort relatif des femelles était en corrélation avec le nombre de petits dans leur portée (τ de Kendall = 0,93, $P = 0,01$).

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Introduction

One aspect of parental care by wolves (*Canis lupus*) is the regurgitation or disgorging of food to family members. After feeding, wolves regurgitate to their pups or to the breeding female (Murie 1944; Young and Goldman 1944). Expectant recipients excitedly solicit regurgitation by licking and sniffing a wolf's muzzle (Murie 1944; Rutter and Pimlott 1968). The wolf either regurgitates directly or rushes up to 400 m away and then regurgitates, sometimes repeatedly (Mech 1988). Food transferred via regurgitation supplements food carried in the mouth (Murie 1944; Haber 1977; Mech 1988; Packard et al. 1992).

Only incidental observations of regurgitation by free-ranging wolves have been reported, so detailed information comes only from captive packs. When offspring from previous litters remain with a breeding pair, they may both solicit and deliver regurgitations (Fentress and Ryon 1982; Packard et al. 1992; Mech 1995*a*). In two packs, only the breeding male did not solicit regurgitation (Fentress et al. 1978; Fentress and Ryon 1982; Paquet et al. 1982). In a pack with two breeding females, the breeding male regurgitated to all but an immature yearling female (Paquet et al. 1982). In another family, the breeding male regurgitated to yearlings but not to the pregnant female; after parturition he fed the lactating mother until the pups emerged from the den, then he fed the pups (Fentress et al. 1978). Eventually the yearlings fed the pups but not the mother, and the yearlings were often fed by the adults (Fentress and Ryon 1982). During a summer when the free-ranging wolves in the present study produced no pups, the breeding female regurgitated to a yearling (Mech 1995*a*). The results of two field studies suggested that some yearlings may be more likely to intercept than to deliver regurgitations (Harrington and Mech 1982; Ballard et al. 1991). This raised the question of whether offspring that remain with the family may compete more than contribute.

We present the first detailed description and analysis of regurgitation behavior in a free-ranging wolf pack and test the hypothesis that auxiliary pack members receive more regurgitations than they deliver. We also focused on (*i*) a comparison of the regurgitation behavior of the breeding female and breeding male, (*ii*) which individuals donated and received regurgitations, and (*iii*) correlations between litter size and relative effort by the breeding female.

Methods

This study was conducted on Ellesmere Island, North West Territories, Canada (80°N, 86°W). There, wolves prey on arctic hares (*Lepus arcticus*), muskoxen (*Ovibos moschatus*), and Peary caribou (*Rangifer tarandus pearyi*) (Mech 1988). During 1986, the senior author habituated a pack of wolves to his presence and reinforced the habituation each summer (Mech 1988, 1995*a*, 1995*b*; Packard

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Table 1. Composition of the study pack of wolves.

		Breeders		Auxiliaries	
Year	No. of pups	Female	Male	Female	Male
1988	4	Mom	Left Shoulder	Whitey	Grey Back
1990	1	Whitey	Left Shoulder	Mom	—
1991	2	Whitey	Left Shoulder	Mom	—
1992	3	Whitey	Left Shoulder	—	—
1994	1	Whitey	Left Shoulder	Explorer	Grey Back II
1996	2	Whitey	Left Shoulder	—	—

Note: No data were collected in 1989; no pups were produced in 1993 or 1995.

Table 2. Numbers[a] of regurgitations by wolves of various classes.

	Breeders[a]		Auxiliaries		
Year	Female	Male	Female	Male	Total
1988	46[b] (47)	18[c] (18)	21 (21)	13[c] (13)	98
1990	2 (10)	15 (75)	3 (15)	—	20
1991	3 (38)	4 (50)	1 (13)	—	8
1992	6 (50)	6 (50)	—	—	12
1994	0	8 (40)	3 (15)	6 (30)	17
1996	4 (31)	9 (69)	—	—	13
Total	64	60	28	19	168
Mean[d]	10 (27)	10 (27)	7 (19)	10 (26)	9
Mean[e]	6 (24)	7 (31)	5 (20)	6 (24)	6

Note: A few regurgitations in a given bout may have been missed because of occasional visual obstruction during observation. Values in parentheses are percentages.

[a]No significant difference between male and female over 6 years (Wilcoxon's signed-rank test, $z = -0.67$, $P = 0.5$).

[b]Value contributed to significance of χ^2 goodness-of-fit test ($\chi^2 = 26.49$, $P < 0.001$); higher than expected by chance (Freeman–Tukey deviate, $z = 3.69$).

[c]Values lower than expected by chance ($z < 12.961$).

[d]Average number of regurgitations per wolf per year.

[e]Average number of regurgitation bouts per wolf per year.

et al. 1992). In addition to hunting, the pack we observed also scavenged from the refuse pile of a weather station. The wolf pack frequented the same area each summer and used the same den (Mech and Packard 1990) or nearby dens (Mech 1995*b*) during 5 of the 7 summers when they produced pups during this study. The habituation allowed us to watch the wolves regularly from distances of 10–100 m.

Data for the present study were collected from 1988 through 1996. We began observing between 14 and 28 June (when the pups were 10–25 days old) and ended in early August. We did not attempt to randomly sample behaviors; rather, we observed as many food deliveries as we could. Although our efforts varied with logistics and weather each year, general procedures were the same except in 1988, when we also observed continuously for one 5-day period.

We identified adult-sized wolves on the basis of gender (from the urination posture), behavior toward the observer, fur coloration, and such individual features as a missing tooth, ear notch, and scars (Mech 1995*b*). Pups were not individually recognizable, but as yearlings they demonstrated the habituation they had received as pups. Nonhabituated wolves from other packs fled when approached (Mech 1995*b*).

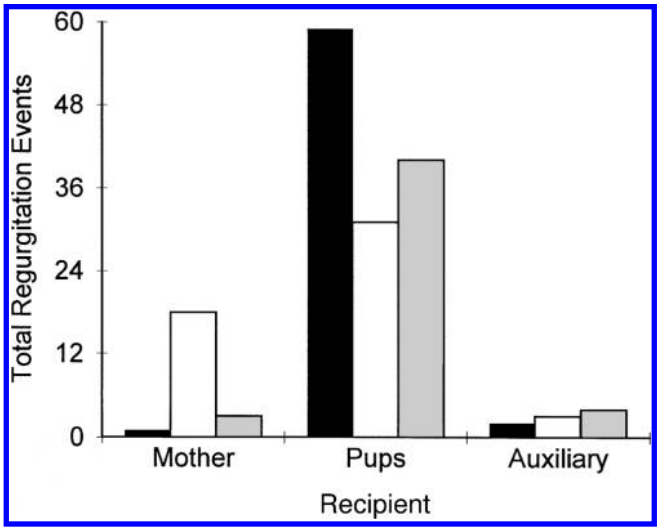
Over 9 years, six adult-sized wolves were observed with six litters (Table 1). "Mom" produced pups from 1986 through 1989, and she remained as an auxiliary when post-reproductive, behavior we have not seen documented elsewhere. Her daughter, "Whitey," replaced Mom as breeder from 1990 through 1996 (Mech 1995*b*; L.D. Mech, unpublished data). No other offspring remained for more than 3 summers after their birth year. Presumably they dispersed or died (Mech et al. 1998).

Our observations were made at several home sites unobscured by vegetation. All behavior was recorded from the time a foraging wolf returned until it disappeared or observations were terminated. Each time a wolf regurgitated was one event, and all the regurgitation events after a return constituted a regurgitation bout. Only five observations of regurgitation bouts were incomplete (e.g., the wolf went behind a rock or ridge). In three cases when wolves regurgitated into a cache, the senior author later dug up the cache and weighed the contents.

Results

We recorded 168 regurgitations in 114 bouts (Table 2). Usually, when a foraging wolf returned to the den area it was eagerly met by the pups and often by all the members present. When it regurgitated, sometimes more than one class of pack members fed. In 76% of the bouts, arriving wolves regurgitated where they were met, and in another 11% they were followed by the recipient(s) for 10–50 m before regurgitating. At other times they were followed up to 800 m. Wolves regurgitated only once in 61% of the bouts, twice in 24%, and three to five times in 12%, over periods of 5–35 min. Often subsequent regurgitations followed solicitation by recipients, but at other times the regurgitator spontaneously re-approached recipients as though inviting

Fig. 1. Distribution of donors and recipients of regurgitations in a wolf pack observed for 6 summers. Donors are denoted as follows: the breeding female by solid bars; the breeding male by open bars; and auxiliaries by shaded bars. Recipient distribution differed from random (G^2 = 30.76, 4 df, P > 0.001). The breeding female regurgitated more to the pups (z = 2.88) and the breeding male regurgitated more to the breeding female (z = 4.4).



solicitation. The number of regurgitations per bout matched the number of recipients in only 7 of 114 bouts. Although the number of regurgitations per bout ranged from 1 to 5, the proportion of regurgitations to bouts did not vary among individuals. Individuals of all classes, the breeding male and female and auxiliaries, occasionally reingested their own regurgitations.

Regurgitation into caches was rare (4 of 171 events). The masses of four regurgitations recorded from three caches were as follows: 2.5 kg (two regurgitations that included 30 chunks averaging 80 g) and 1.1 kg by the breeding male and 1.4 kg by the breeding female. Thus, the average was 1.25 kg per regurgitation. The breeding male's caching took place during the first half of summer.

Overall, the number of regurgitations by individuals of both sexes and both roles were similar (Table 2). The pups were the main recipients of regurgitations (81%; Fig. 1), receiving more than the breeding female (14%) or auxiliaries (6%). We never saw the breeding male soliciting regurgitation.

The breeding female and auxiliaries regurgitated mostly to the pups, but the breeding female also regurgitated to auxiliaries and into a cache (Fig. 1). Only a few times did we see the auxiliaries regurgitating to other auxiliaries or to the breeding female. Auxiliaries sometimes partook of the regurgitated food delivered by others to pups, littermates, and the breeding female. Approximately 57% of the regurgitations by the breeding male were to pups, 32% to the breeding female, 5% to auxiliaries, and 5% into caches. The breeding male regurgitated more often to the pups in late summer (74%) than in early summer (41%), when he fed the female more (χ^2 = 6.10; P = 0.01; n = 56).

Across 6 years, the ratio of regurgitations by the breeding female to total regurgitations by all pack members was positively correlated with litter size (Kendall's τ = 0.93, P = 0.01), but not to pack size (Kendall's τ = –1.49, P = 7.1). Apparently the presence of more auxiliaries did not reduce the regurgitation effort by the breeding female.

Discussion

This study adds considerable detail to anecdotal reports that wolves transport food in their stomach and regurgitate it to nursing females and pups. It also confirms observations that in captive wolves, yearlings and adult pack members transfer food via regurgitation to the breeding female, pups, and nonbreeders, though the recipients are usually only the breeding female and pups, and that only the breeders regurgitate into caches (Fentress et al. 1978; Fentress and Ryan 1982; Paquet et al. 1982).

Our results do not support the hypothesis that auxiliary wolves compete more than they contribute, at least during the first 2 months of pup development, (Harrington and Mech 1982; Ballard et al. 1991). Instances of auxiliaries receiving regurgitations from the breeding pair and other auxiliaries were infrequent during both the initial and the second transition phases of parental care, when pups actively solicited regurgitation and switched from milk to solid food (Packard et al. 1992). Rather, our auxiliaries appeared to have helped more than they hindered food transfer. Such help is in keeping with the kin-selection hypothesis (Williams 1966).

Assuming that, on average, 1.25 kg of food is delivered per regurgitation, an estimate of food delivered per bout would be 1.25–7.25 kg. Since the proportion of regurgitations per bout averaged 1.5, our best estimate of the amount of food per bout would be 2.2 kg. This calculation assumes that the amount regurgitated to pups is the same as the amount regurgitated into caches, but this assumption needs testing.

Fentress and Ryon (1982) hypothesized that wolves can selectively transfer food via regurgitation to whichever individuals they wish. Our data support this hypothesis in the probabilistic sense: given that a regurgitation was donated by individuals of a particular age–sex class, recipients were not equiprobable. More regurgitations by a breeding male were received by a breeding female and more regurgitations by a breeding female were received by the pups than in the pattern shown by auxiliaries. However, such probabilities do not consider differential rates and intensities of solicitation, which are difficult to quantify, so they do not demonstrate control in the sense of intentionality on the part of donors.

Integrating observations made in the field and in captivity, we hypothesize that (*i*) over the duration of a pair bond, male and female do not differ in regurgitation effort, although they may differ during specific years, (*ii*) the recipients are usually the breeding female and the pups, seldom the auxiliaries, and rarely, if ever, the breeding male, (*iii*) litter size affects regurgitation effort by the breeding female, and (*iv*) members of the breeding pair are more likely than auxiliaries to cache regurgitant matter during the initial phase of lactation, when the pups are still in the den.

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