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Citation

Haig, David. 2008. Huddling: brown fat, genomic imprinting and the warm inner glow." Current Biology 18(4): R172-R174.

Published Version

doi:10.1016/j.cub.2007.12.040

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Huddling: brown fat, genomic imprinting, and the warm inner glow

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Huddling for warmth is a common cooperative behavior. Heat generation within a huddle is a public good with a private cost. Therefore, cooperators are potentially vulnerable to exploitation by free-riders. Recent studies in penguins and rabbits illustrate the benefits of huddling and the temptation to defect. Effects of imprinted genes in brown adipose tissue suggest that non-shivering thermogenesis is an arena for intragenomic conflict.

“... if two lie together, then they have heat; but how can one be warm alone?”
(Ecclesiastes 4:11)

Huddling is a simple and widespread cooperative behavior of inactive homeotherms. In cold environments, huddling reduces heat loss by reducing each individual's exposed surface area. Moreover, animals that congregate in an enclosed space can raise the ambient temperature more effectively than an individual acting alone, reducing each individual's heat loss per unit of exposed surface. Energy savings may be substantial. For example, 45 *Eptesicus fuscus* (large brown bats) huddled in a tree cavity expend less than half the energy of the same number, each roosting alone [1].

Within a huddle, the fuel consumed by thermogenesis is a direct personal cost to each individual but the benefits are shared. Social thermoregulation is therefore vulnerable to exploitation by free-riders who skimp on their share of the heating bill. A recent study of emperor penguins reveals the interplay of cooperation and conflict during huddling. Another study by the same group quantifies the benefits of huddling in litters of rabbits.

Paternal endurance and sib conclaves

Male emperor penguins endure a four-month fast through the depth of the Antarctic winter. During this fast, males live off fat reserves while incubating an egg and then feeding the newly-hatched chick. Males huddle in large groups, especially in bad weather. This allows them to reduce heating costs while maintaining high incubation temperatures. Huddling is essential for successful reproduction because males have insufficient reserves to survive winter on their own [2,3].

Gilbert and colleagues [3] monitored core and subcutaneous body temperatures of five male emperor penguins during their winter fast. Fortuitously, one male lost his egg during a blizzard (after 20 days incubation). The four males who retained their eggs maintained high core temperatures while huddling ($36.9 \pm 0.3^{\circ}\text{C}$). The fifth male maintained a high core temperature before losing his egg but thereafter reduced his core temperature while huddling ($35.5 \pm 0.4^{\circ}\text{C}$; range 32.8°C to 37.4°C), thereby becoming a net recipient of heat from his warmer neighbors. (His core temperature would often have been cooler than the surface temperature of his neighbors.) A plausible interpretation is that loss of his egg shifted the marginal costs and benefits of thermogenesis. Once freed from the constraint of providing heat to a developing chick, this male was able to exploit heat production by other males who still incubated eggs.

Huddling is particularly important for young birds and mammals with high surface area to volume ratios. Huddling behavior has been extensively studied in rat litters [4, 5]. Pups snuggle closer together at colder temperatures, causing the aggregate surface area of a huddle to expand as temperature rises and contract as temperature falls. During contraction, outer pups attempt to wriggle into the center, creating 'convection currents' in which individual pups circulate between the surface and center of the pile. When thermogenesis was pharmacologically inhibited in one or more pups, huddles were stable at 15°C if all pups were treated or no pups were treated, but mixed huddles disintegrated [6].

Rabbit mothers, unlike rat dams, suckle their pups for 3-5 minutes, once a day, but do not otherwise interact with their offspring. Pups huddle in the absence of their mother and raise their body temperature shortly before her predicted return. Gilbert and colleagues [7] exploited these unusual features of maternal care to assess benefits of huddling. Rabbit pups were kept at $23\text{-}24^{\circ}\text{C}$ in groups of one, two, four, or eight but were returned to their original litters for suckling. In comparison to pups raised alone, pups from groups of eight used 40% less energy between days 3—5 and accumulated more fat by day 12. Pups

reared alone failed to raise their body temperature before their mother's return and consumed less milk during her brief visits. Thus energetic savings from huddling were converted into greater access to maternal resources.

Pups help to reduce each other's heating costs but are also competitors for milk. The evolutionary balance between these forces will be determined, in part, by the extent of gene sharing among huddle-mates.

Huddling with relatives

Consider the fate of a newly-arisen (and thereby rare) allele that reduces thermogenesis in a population in which most individuals contribute to social heating. If huddles consist of non-relatives, then carriers of the rare allele will be the only members of their huddle to reduce thermogenesis. In this case, an allele carrier would reduce his own costs of thermogenesis while continuing to receive heat from the rest of the group. If, on the other hand, huddles consist of full-sibs, then an allele carrier would reduce his heating costs but would also lose heat contributions from half the other members of the huddle who carry a copy of the same allele. Other things being equal, alleles for free-loading are more likely to invade a population (and spread to fixation) if huddles consist of non-relatives.

Degrees of relatedness can vary among individuals within huddles. In this case, individuals of lower-than-average relatedness are expected to exploit the thermogenesis of individuals of higher-than-average relatedness. Groups of up to 20 alpine marmots hibernate together through the winter. When the huddle contains juveniles, winter weight loss increases for older sibs of the litter but decreases for less-related individuals [8]. This suggests that older sibs increase thermogenesis to enhance the survival of juveniles and less-related individuals benefit by reducing their own heat production.

Of particular interest, degrees of relatedness within a huddle may differ for genes of maternal and paternal origin. For example, in a multiple-paternity litter, more individuals will share genes of maternal origin than will share genes of paternal origin. Therefore, maternally-expressed imprinted genes are predicted to promote higher contributions to communal heating than the level favored by paternally-expressed imprinted genes [9].

Brown fat and genomic imprinting

Young mammals generate heat by non-shivering thermogenesis in brown adipocytes [10]. At least three imprinted loci influence this process in mice. Two paternally-expressed loci, *Pref1/Dlk1* and *Necdin* [11, 12], reduce the size of the furnace by inhibiting differentiation of preadipocytes into brown adipocytes [13]. The third imprinted locus, *GNAS*, modulates the heat output of individual cells. Sympathetic activation of β -adrenergic receptors on the surface of brown adipocytes releases the G protein α stimulatory subunit ($G\alpha_s$) which initiates cellular events that activate thermogenesis [10]. Both alleles produce $G\alpha_s$ in most tissues, but the maternally-derived allele is preferentially expressed in brown adipose tissue [14]. $XL\alpha_s$ ("extra large" α_s) is produced by the paternally-derived *GNAS* allele and antagonizes the effects of $G\alpha_s$ in brown adipose tissue [15]. Thus, *GNAS* produces both a maternally-expressed promoter and a paternally-expressed inhibitor of non-shivering thermogenesis. This is the pattern predicted if matrilineal relatedness exceeds patrilineal relatedness within huddles. Future studies will test whether this pattern is maintained at other imprinted loci.

Evolution of cooperation

The evolution of cooperation has been a major area of theoretical and empirical research in evolutionary biology, but with a perceived need to exploit new study systems for testing theoretical models [16]. Social thermogenesis has certain advantages for studying the stability and breakdown of cooperation. Huddles are spatially localized, and fitness-related variables (temperature, body weight, milk consumption) are easily measured. Moreover, pharmacological and genetic interventions are available to adjust how much particular individuals contribute to the collective good.

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