One for all and all for one: the energetic benefits of huddling in endotherms

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ABSTRACT

Huddling can be defined as "an active and close aggregation of animals". It is a cooperative group behaviour, permitting individuals involved in social thermoregulation to minimize heat loss and thereby lower their energy expenditure, and possibly allowing them to reallocate the saved energy to other functions such as growth or reproduction. Huddling is especially important in the case of animals faced with high heat loss due to a high surface-to-volume ratio, poor insulation, or living in cold environments. Although numerous experimental studies have focused on the huddling behaviour of a wide range of species, to our knowledge, this is the first attempt to review the various implications of this widely used behavioural strategy.

Huddling allows individuals to maximise energy savings by (1) decreasing their cold-exposed body surface area, (2) reducing their heat loss through warming of ambient temperatures surrounding the group, and (3) eventually lowering their body temperature through physiological processes. Huddling provides substantial energy savings and is estimated to reduce energy expenditure by between 6 and 53%. Broad variations in the energetic benefits of huddling depend on the number of individuals and species involved in huddles, the ambient temperatures to which individuals are exposed and the density of the aggregations. It has been shown that huddling individuals have increased survival, a lower food intake, a decreased body mass loss, increased growth rate, reduced water loss, and/or a more constant body temperature together with a significant reduction in metabolic rate. Though huddling has been studied widely, this review reveals the intricacies of this adaptive behaviour.

Key words: huddling, group, social behaviour, thermoregulation, energy conservation, ambient temperature, mammals, birds.

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I. INTRODUCTION

During evolution, organisms become adapted to changing environments, notably through optimisation of their energy balance due to morphological, physiological, and behavioural adaptations. Energy conservation allows organisms to allocate energy to other functions, such as growth or reproduction, enhancing their survival and fitness, especially where there is seasonality in energy supply. Several energy conservation strategies have evolved in endothermic mammals and birds which are capable of producing heat endogenously and maintaining a constant and high body temperature over a wide range of environmental temperatures. Physiological strategies, such as daily torpor and hibernation, are the most dramatic, producing hypometabolism through a gradual reduction in body temperature (for review see Geiser, 2004; Heldmaier, Ortmann & Elvert, 2004). However, these major strategies are associated with periods of rest and are largely incompatible with other activities, such as reproduction or growth, which need to be delayed in time. Another widely used energy conservation strategy is huddling. A major advantage of this strategy is that it can be associated with other active behaviours, and with the maintenance of the high body temperature necessary for growth or reproduction in these species. This behavioural strategy is thus widely used by mammals and birds.

Thermoregulation in endotherms is defined as the regulation of body temperature, through homeostatic mechanisms controlling heat production in relation to heat loss, to maintain a high and relatively constant value independent of changes in environmental temperature (McNab, 2002).

Social thermoregulation refers to the ability of some species to use sociality and grouping to regulate their body temperature. The major behaviour linking grouping to thermoregulation is "huddling". Other terms have been used depending on the characteristics of the groups, their density, duration, and the number of individuals or species involved: clustering, aggregation, clumping, grouping, communal nesting or nest grouping, communal roosting and crèching. Alberts (1978*a*) proposed the first definition of huddling, during an experimental study on rats: "huddling is the behaviour that leads to the formation and maintenance of the litter aggregate, and, similarly, produces the social clumps of adult rats observed under group-living conditions". Martin, Fiorentini & Connors (1980) proposed a broader definition: "aggregation is a behavioural pattern common to many small mammals. Often referred to as huddling, it is especially apparent at low ambient temperatures." Following an extensive empirical study, Canals (1998) defines huddling as "the grouping of individuals close together to keep warm." Hayes (2000) uses the terms "huddling" or "aggregative behaviour" to describe groups of individuals engaged in behavioural thermoregulation, *i.e.* "huddling groups" would correspond to an active aggregation. An agreed definition of huddling is therefore "an active and close aggregation of animals". In addition to this broad definition, a more precise notion of "huddling" refers to the fact that the grouped animals are involved in social thermoregulation, in order to keep warm. We chose to focus our review on this function.

Numerous experimental studies have focused on huddling behaviour in a broad range of species, mainly exploring

energy-saving benefits associated with adaptive questions specific to the species and their environmental constraints. However, to our knowledge, this is the first attempt to review the various implications of this widely used behavioural strategy. Although huddling also occurs in ectothermic vertebrates and invertebrates [thick-tailed gecko *Nephrurus milii* (Shah *et al.*, 2003), honeybee *Apis mellifera* (Grodzicki & Caputa, 2005)], we have chosen to restrict this review to endothermic mammals and birds. We aim to provide an overview of the determinants enhancing huddle formation, the factors explaining the energetic savings associated with huddling, the energetic benefits of huddling in a range of species, and finally the causes of variation in these energy savings.

II. DETERMINANTS OF HUDDLING

(1) Metabolism and thermoregulation

Thermoregulation encompasses thermogenesis (*i.e.* heat produced from the transformation of energy from food or body reserves) and thermolysis (*i.e.* heat loss from the organism to the environment) (Schmidt-Nielsen, 1997). Thus body temperature depends on the equilibrium between heat production and heat loss. Heat can be dissipated through conduction, convection, radiation and evaporation (McNab, 1974). The body temperature of a homeotherm is maintained at a high and relatively constant level, even at low ambient temperatures, which is metabolically costly (McNab, 1974; Schmidt-Nielsen, 1997).

During cold exposure, based on Fourier's Law of heat flow, endotherms increase their metabolic heat production in order to maintain a constant body temperature, as described by the equation: $MR = C(T_b - T_a)$, where MR is metabolic heat production (W), C is thermal conductance (W°C^{-1}), T_b is body temperature (°C), and T_a is ambient temperature (°C) (Scholander *et al.*, 1950; Heldmaier & Ruf, 1992). Total heat loss therefore depends on two factors, the temperature gradient between body and ambient temperatures, and the thermal conductance of the organism. High heat loss will occur if the gradient between ambient and body temperature is high, *e.g.* for animals living in cold environments. Overall thermal conductance is dependent on (1) the total surface area of the animal exposed to the environment and (2) the insulation properties of this body surface. Many species exhibit morphological adaptations that enhance the insulation properties of their body surface. For example, the highly insulative properties of the plumage of the emperor penguin (*Aptenodytes forsteri*) is estimated to provide 80% of the total insulation required to tolerate the severe climatic conditions of the Antarctic continent (Le Maho, 1977), the other 20% being attributed to adipose tissue. In addition, the body surface exposed to the environment will determine the extent of the thermal fluxes. The surface area to volume ratio $S{:}V$ will vary among animals depending on their body size: S is proportional to L^2 (where L is length) and V to L^3,

therefore S is proportional to $V^{2/3}$, *i.e.* the body volume$^{0.67}$ or body mass$^{0.67}$. Thus, as the volume of a body increases, its surface area does not increase in the same proportion, but in smaller increments. The surface-area-to-volume ratio is therefore higher for small compared to large animals and their endothermic costs are hence greater; they need to maintain a relatively higher metabolic heat production, and consequently a higher mass-specific metabolic rate to maintain the same body temperature. Indeed, a recent study accounting for variation associated with body temperature, digestive state, and phylogeny, found that mammalian basal metabolic rate is proportional to body mass$^{0.67}$ (White & Seymour, 2003); for captive birds, body metabolic rate is proportional to body mass$^{0.67}$ whereas it is body mass$^{0.74}$ for wild-caught birds (McKechnie, Freckletonn & Jetzn, 2006).

Basal (or resting) metabolic rate is defined as the minimum maintenance metabolism of a resting endotherm, at thermoneutral environmental temperatures and in the absence of thermoregulatory, digestive, circadian or other increments in metabolic heat production (McNab, 1997; Schmidt-Nielsen, 1997). Metabolic rate is minimal and constant within an animal's thermoneutral zone (TNZ), where heat loss is also minimal (Fig. 1; Scholander *et al.*, 1950; Satinoff, 1996). The TNZ ranges from the lower critical temperature (LCT) to the upper critical temperature (UCT), within which extremes no extra energy is required to maintain a constant body temperature. For ambient temperatures higher than the UCT, heat loss is enhanced (particularly through evaporation) and for temperatures lower than the LCT, thermogenesis, and thus metabolic rate, is increased, though shivering, enhanced locomotor activity, or brown fat thermogenesis (Fig. 1; Satinoff, 1996). Measurements of field metabolic rate (FMR) quantify total energy requirements and are used to elucidate patterns of energy allocation in free-ranging animals (*e.g.* Nagy, 1987).

There are several methods by which the costs of thermogenesis can be reduced, especially during periods of prolonged cold. First, the gradient between body and ambient temperature can be minimized *via* physiological adaptations such as increased vasoconstriction to reduce the temperature of the skin surface. Many species also increase the insulation properties of their plumage or fur during the cold season, in order to minimize heat loss (Walsberg, 1991; Piersma, Cadee & Daan, 1995). Secondly, they can lower their body temperature by entering torpor or hibernation (Geiser, 2004; Heldmaier *et al.*, 2004). Third, behavioural thermoregulatory adaptations can increase the environmental temperature to within the thermoneutral zone, for example by selecting sheltered sites, where environmental conditions are milder. Such favoured sites will eventually be occupied by several individuals, resulting in the warming of the local microclimate (Hayes, Speakman & Racey, 1992; Willis & Brigham, 2007). Many species migrate to reach milder habitats in winter. Finally, organisms may minimize energy costs by reducing the exposed body surface area, through individual postures (*e.g.* vultures, Ward *et al.*, 2008), or by huddling together.
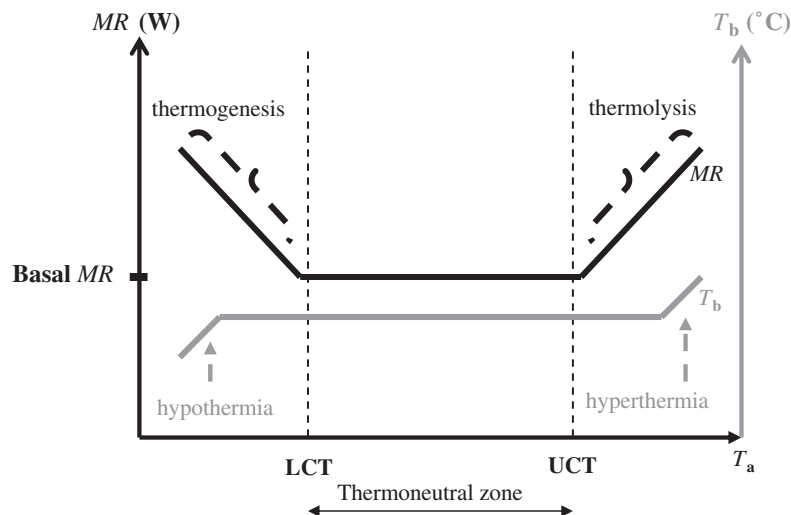
Fig. 1. Metabolic rate (*MR*) and body temperature (*T*$_b$) as a function of ambient temperature (*T*$_a$), showing positions of lower critical temperature (LCT) and upper critical temperature (UCT).

(2) Factors influencing huddling

Huddling is used by a wide variety of species (Table 1). To our knowledge, 67 mammal species from 20 families and 25 bird species from 18 families use huddling. Here we include species that have been documented considering their capacity to huddle, *i.e.* to form an active and close aggregation, mostly in relation to cold temperatures, this behaviour bringing thermoregulatory benefits for individuals involved in the groups. We therefore did not include species that develop strong links between adults and offspring that result in close contact, such as newborn primates. The advantages of close contact for mother and offspring in primates are partly social, linked to the fact that the young suckle frequently: thermoregulatory advantages mainly benefit the infant. No existing study has attempted to dissociate their respective effects. In humans, there is no scientific study linking huddling and thermoregulatory benefits. Indeed, during cold exposure, humans mostly adopt postural adaptations, seek shelter, use protective clothing, *etc.* before using social thermoregulation (Mäkinen, 2007). However, huddling is a behaviour that humans in groups or a family may adopt, when they are unable to use other ways to warm themselves. We know of no reports considering the energetic benefits of this behaviour.

Huddling as a conservation strategy is used almost as widely as daily torpor and hibernation strategies: Geiser (2004) provided a list of 76 daily heterotherms and hibernators among mammals and 16 bird species. Among those daily heterotherms, six mammal and one bird species also form huddling groups, while six hibernating mammals use both energy-saving strategies.

(a) Ecological factors

Ecological factors, such as severe climatic conditions, enhance huddling. Some species may be subject to periods of cold, commonly during the winter season, in which temperatures fall below their lower critical temperature. Many rodents use huddling during the winter (Table 1), and it is used as an adaptive strategy by species that have colonized particularly cold habitats. For example, snow geese (*Chen caerulescens atlantica*) goslings hatching during the high Arctic summer (Fortin, Gauthier & Larochelle, 2000) and king penguin (*Aptenodytes patagonicus*) chicks fasting during the subantarctic winter (Le Bohec, Gauthier-Clerc & Le Maho, 2005) use huddling within their crèches. The most extreme example of cold adaptation is the emperor penguin (*Aptenodytes forsteri*), which breeds during the austral winter at the border of the Antarctic continent. Adults, and especially males during incubation, huddle together in order to save energy during their four-month fast (Prévost, 1961; Ancel *et al.*, 1997; Gilbert *et al.*, 2008*a*).

Even though it is generally assumed that the prevalence of huddling increases during unfavourable climatic conditions, only a few studies have investigated variables such as occurrence of huddle formation, number of huddles formed, duration of huddling, group density, or number of individuals involved in huddles, as a function of ambient temperature (Smith, 1972; Batchelder *et al.*, 1983; Takahashi, 1997; Le Bohec *et al.*, 2005; Gilbert *et al.*, 2008*b*; Table 2). Gebczynski (1969) noted that at ambient temperatures of 25°C, bank voles (*Clethrionomys glareolus*) showed increased activity and do not huddle, but when exposed to lower ambient temperatures (14°C and 3°C), they decreased their activity and huddled in the nest. Similarly, redfronted lemurs (*Eulemur fulvus rufus*) respond to a reduction in ambient temperature with decreased activity and huddling (Ostner, 2002). Grubb (1973) noted that tree swallows (*Iridoprocne bicolor*) form groups and decrease their inter-individual distance in low ambient temperatures. Meservey & Kraus (1976) reported the clustering of three species of swallows (*Petrochelidon pyrrhonota*, *Hirundo rustica*, *Iridoprocne bicolor*) exposed to

Table 1. A list of species using huddling, either in natural or experimental conditions, as young and/or adult individuals. Birds are highlighted in grey for ease of comparison with Tables 2 and 3. Classification is according to Myers *et al.* (2008).

Order	Family	Subfamily	Genus/species	Common name	References
Class : Mammals					
Artiodactyla	Suidae	Suinae	*Sus scrofa domesticus* (Linnaeus, 1758)	Domestic pig	Hrupka *et al.* (2000); Mount (1960)
Carnivora	Procyonidae		*Procyon lotor* (Linnaeus, 1758)	Northern raccoon	Mech & Turkowski (1967)
	Odobenidae		*Odobenus rosmarus* (Linnaeus, 1758)	Walrus	Miller (1976); Riedman (1990)
	Otariidae		*Arctocephalus pusillus* (Schreber, 1775)	South African and Australian fur seal	Riedman (1990)
			Callorhinus ursinus (Linnaeus, 1758)	Northern fur seal	Riedman (1990)
			Eumetopias jubatus (Schreber, 1776)	Steller sea lion	Riedman (1990)
			Otaria flavescens (Shaw, 1800)	Southern sea lion	Riedman (1990)
			Phocarctos hookeri (Gray, 1844)	New Zealand sea lion	Riedman (1990)
			Zalophus californianus (Lesson, 1828)	California sea lion	Riedman (1990)
	Phocidae		*Mirounga angustirostris* (Gill, 1866)	Northern elephant seal	Riedman (1990)
			Mirounga leonina (Linnaeus, 1758)	Southern elephant seal	Riedman (1990)
			Phoca vitulina (Linnaeus, 1758)	Harbor seal	Riedman (1990)
Chiroptera	Phyllostomidae	Glossophaginae	*Glossophaga soricina* (Pallas, 1766)	Pallas's long-tongued bat	Howell (1976)
	Noctilionidae		*Noctilio albiventris* (Desmarest, 1818)	Lesser bulldog bat	Roverud & Chappell (1991)
	Vespertilionidae	Myotinae	*Myotis leibii* (*subulatus*) (Audubon & Bachman, 1842)	Eastern small-footed myotis	Studier *et al.* (1970)
			Myotis lucifugus (LeConte, 1831)	Little brown bat	Studier *et al.* (1970)
			Myotis thysanodes (Miller, 1897)	Fringed myotis	Studier *et al.* (1970)
			Myotis velifer (Allen JA, 1890)	Cave myotis	Studier *et al.* (1970)
			Myotis yumanensis (Allen H, 1864)	Yuma myotis	Studier *et al.* (1970)
		Vespertilioninae	*Eptesicus fuscus* (Palisot de Beauvois, 1796)	Big brown bat	Willis & Brigham (2007)
Dasyuromorphia	Dasyuridae	Sminthopsinae	*Sminthopsis crassicaudata* (Gould, 1844)	Fat-tailed dunnart	Frey (1991)
		Dasyurinae	*Phascogale tapoatafa* (Meyer, 1793)	Brush-tailed phascogale	Rhind (2003)
Didelphimorphia	Didelphidae	Didelphinae	*Thylamys elegans* (Waterhouse, 1839)	Elegant fat-tailed opossum	Canals (1998); Canals *et al.* (1997, 1998)
Lagomorpha	Leporidae		*Oryctolagus cuniculus* (Linnaeus, 1758)	European rabbit	Bautista *et al.* (2003); Gilbert *et al.* (2007*a*)
Primates	Cercopithecidae	Cercopithecinae	*Macaca fuscata* (Blyth, 1875)	Japanese macaque	Takahashi (1997)
			Macaca thibetana (Milne-Edwards, 1870)	Tibetan macaque	Ogawa & Takahashi (2003)
	Cheirogaleidae		*Microcebus murinus* (Miller, 1777)	Gray mouse lemur	Perret (1998)

Table 1. *(cont.)*

Order	Family	Subfamily	Genus/species	Common name	References
			Microcebus ravelobensis (Zimmerman *et al.*, 1998)	Golden-brown mouse lemur	Radespiel *et al.* (2003)
	Lemuridae		*Eulemur fulvus rufus* (Geoffroy E, 1796)	Redfronted lemur	Ostner (2002)
Rodentia	Bathyergidae	Bathyerginae	*Cryptomys damarensis* (Ogilby, 1838)	Damaraland mole rat	Kotze *et al.* (2008)
			Cryptomys hottentotus natalensis (Lesson, 1826)	Natal mole rat	Kotze *et al.* (2008)
		Heterocephalinae	*Heterocephalus glaber* (Rüppel, 1842)	Naked mole rat	Withers & Jarvis (1980); Yahav & Buffenstein (1991)
	Critecidae	Arvicolinae	*Clethrionomys glareolus* (Flowerdew JR & Trout C, 1995)	Bank vole	Gebczynska & Gebczynski, (1971); Gebczynski (1969); Gorecki (1968)
			Microtus agrestis (Linnaeus, 1761)	Short-tailed field vole	Hayes *et al.* (1992)
			Microtus arvalis (Pallas, 1778)	European common vole	Grodzinski *et al.* (1977); Trojan & Wojciechowska (1968)
			Microtus ochrogaster (Wagner, 1842)	Prairie vole	Hayes (2000)
			Microtus oeconomus (Pallas, 1776)	Root vole, tundra vole	Gebczynska (1970)
			Microtus pennsylvanicus (Ord, 1815)	Meadow vole	Berteaux *et al.* (1996); Wiegert (1961)
			Microtus townsendii (Bachman, 1839)	Townsend's vole	Andrews *et al.* (1987)
			Ondatra zibethicus (Linnaeus, 1766)	Muskrat	Bazin & MacArthur (1992); MacArthur *et al.* (1997)
	Critecidae	Cricetinae	*Mesocricetus auratus* (Waterhouse, 1839)	Golden hamster	Sokoloff & Blumberg (2002); Sokoloff *et al.* (2000)
			Phodopus sungorus (Pallas, 1773)	Djungarian dwarf hamster	Kauffman *et al.* (2003); Newkirk *et al.* (1995, 1998)
			Phodopus campbelli (Thomas, 1905)	Campbell's hamster	Newkirk *et al.* (1995, 1998)
	Critecidae	Neotominae	*Ochrotomys nuttalli* (Harlan, 1832)	Golden mouse	Springer *et al.* (1981)
			Peromyscus spp. (Gloger, 1841)	Deer and white-footed mice	Sealander (1952); Vickery & Millar (1984)
			Peromyscus leucopus (Rafinesque, 1818)	White-footed mouse	Vogt & Lynch (1982)
			Peromyscus leucopus noveboracensis (Rafinesque, 1818)	Northern white-footed mouse	Glaser & Lustick (1975); Vogt & Kakooza (1993)
			Peromyscus maniculatus (Wagner, 1845)	Deer mouse	Andrews & Belknap (1986); Crowley & Bovet (1980)

		Reithrodontomys megalotis (Baird, 1857)	Harvest mouse	Pearson (1960)
Critecidae	Sigmodontinae	*Abrothrix andinus* (Philippi, 1858)	Andean mouse	Canals *et al.* (1998)
		Abrothrix lanosus (Thomas, 1897)	Woolly grass mouse	Canals *et al.* (1989, 1998)
		Eligmodontia typus (Cuvier F, 1837)	Highland gerbil mouse	Canals (1998); Canals *et al.* (1997, 1998)
		Eligmodontia puerulus (Philippi, 1896)	Andean gerbil mouse	
		Phyllotis darwini (Waterhouse, 1837)	Leaf-eared mouse	Bozinovic *et al.* (1988); Bustamante *et al.* (2002); Canals (1998); Canals *et al.* (1997, 1998)
Ctenomyidae		*Ctenomys talarum* (Thomas, 1898)	Tuco-tuco	Cutrera *et al.* (2003)
Hystricidae		*Hystrix africaeaustralis* (Peters, 1852)	Cape porcupine	Haim *et al.* (1992)
Muridae	Deomyinae	*Acomys cahirinus* (Geoffrey E, 1803)	Spiny mouse	Matochik (1988); Miele *et al.* (1983)
Muridae	Gerbillinae	*Meriones unguiculatus* (Milne Edwards, 1867)	Mongolian gerbil	Contreras (1984); Martin *et al.* (1980); McManus & Singer (1975)
Muridae	Murinae	*Apodemus agrarius* (Pallas, 1771)	Striped field mouse	Gorecki (1968); Tertil (1972)
		Apodemus flavicollis (Melchior, 1834)	Yellow-necked field mouse	Fedyk (1971)
		Mastacomys fuscus (Thomas, 1882)	Broad-toothed rat	Bubela & Happold (1993)
		Mus musculus (Linnaeus, 1758)	House mouse	Batchelder *et al.* (1983); Bryant & Hails (1975); Canals *et al.* (1997, 1998); Contreras (1984); Martin *et al.* (1980); Prychodko (1958); Stanier (1975)
		Notomys alexis (Thomas, 1922)	Australian hopping mouse	Baudinette (1972)
		Rattus norvegicus (Berkenhout, 1769)	Norway rat	Alberts (1978*a, b*); Sokoloff & Blumberg (2001, 2002); Sokoloff *et al.* (2000)
		Rhabdomys pumilio (Sparrman, 1784)	African four-striped grass mouse	Scantlebury *et al.* (2006)
Sciuridae	Sciurinae	*Glaucomys volans* (Linnaeus, 1758)	Southern flying squirrel	Layne & Mendi (1994)

Table 1. *(cont.)*

Order	Family	Subfamily	Genus/species	Common name	References
	Sciuridae	Xerinae	*Marmota marmota* (Linnaeus, 1758)	Alpine marmot	Arnold (1988)
			Marmota spp. (Blumenbach, 1779)	Marmots	Arnold (1993); Armitage & Woods (2003)
			Marmota flaviventris (Audubon & Bachman, 1841)	Yellow-bellied marmot	Armitage & Woods (2003)
			Ammospermophilus leucurus (Merriam, 1889)	Antelope ground squirrel	Karasov (1983)
Class : Birds					
Anseriformes	Anatidae	Anserinae	*Chen caerulescens atlantica* (Linnaeus, 1758)	Snow goose	Fortin *et al.* (2000)
Coliiformes	Coliidae		*Colius colius* (Linnaeus, 1758)	White-backed mousebird	McKechnie & Lovegrove (2001); McKechnie *et al.* (2004)
			Colius striatus (Gmelin, 1789)	Speckled mousebird	Brown & Foster (1992)
Coraciiformes	Phoeniculidae		*Phoeniculus purpureus* (Miller JF, 1784)	Green woodhoopoe; red-billed woodhoopoe	Du Plessis & Williams (1994); Ligon *et al.* (1988); Boix-Hinzen & Lovegrove (1998)
Galliformes	Phasianidae	Perdicinae	*Perdix perdix* (Linnaeus, 1758)	Grey partridge	Putaala *et al.* (1995)
	Odontophoridae		*Colinus virginianus* (Linnaeus, 1758)	Bobwhite quail	Case (1973); Gerstell (1939)
Passeriformes	Aegithalidae		*Psaltriparus minimus* (Townsend, 1837)	Common bushtit	Chaplin (1982); Smith (1972)
			Aegithalos caudatus (Linnaeus, 1758)	Long-tailed tit	Hatchwell *et al.* (2009)
	Estrildidae		*Lonchura cucullata* (Swainson, 1837)	Bronze mannikin	Calf *et al.* (2002)
Passeriformes	Hirundinidae		*Iridoprocne bicolor* (Vieillot, 1808)	Tree swallow	Grubb (1973); Meservey & Kraus (1976)
			Hirundo rustica (Linnaeus, 1758)	Barn swallow	
			Petrochelidon pyrrhonota (Vieillot, 1817)	Cliff swallow	
	Meliphagidae		*Melithreptus lunatus* (Vieillot, 1802)	White-naped honeyeater	MacMillen (1984)
			Phylidonyris niger (Bechstein, 1811)	White-cheeked honeyeater	
	Passeridae		*Passer domesticus* (Linnaeus, 1758)	House sparrow	Beal (1978)
	Polioptilidae		*Polioptila melanura* (Lawrence, 1857)	Black-tailed gnatcatcher	Walsberg (1990)
	Neosittidae		*Daphoenositta chrysoptera* (Latham, 1802)	Varied sitella	Noske (1985)
	Sturnidae		*Sturnus vulgaris* (Linnaeus, 1758)	Common starling	Brenner (1965)
	Troglodytidae		*Thryothorus ludovicianus* (Latham, 1790)	Carolina wren	Labisky & Arnett (2006)
Pelecaniformes	Pelecanidae		*Pelecanus erythrorhynchos* (Gmelin, 1789)	American white pelican	Evans (1984)
	Phalacrocoracidae		*Phalacrocorax penicillatus* (Brandt, 1837)	Brandt's cormorant	Carter & Hobson (1988)

Piciformes	Picidae	*Melanerpes formicivorus* (Swainson, 1827)	Acorn woodpecker	Du Plessis *et al.* (1994)
Sphenisciformes	Spheniscidae	*Aptenodytes forsteri* (Gray, 1844)	Emperor penguin	Ancel *et al.* (1997); Gilbert *et al.* (2008*a*); Prévost (1961)
		Aptenodytes patagonicus (Miller JF, 1778)	King penguin	Le Bohec *et al.* (2005)
		Pygoscelis adeliae (Hombron & Jacquinot, 1841)	Adélie penguin	Davis (1982)

Table 2. Effect of climatic conditions on huddling. Birds are highlighted in grey for ease of comparison with Tables 1 and 3.

Species	Variable measured	Effect	Reference
House mouse *Mus musculus*	Total huddling during the dark phase	increased by 22% (5°C *versus* 26°C)	Batchelder *et al.* (1983)
	Number of huddles per night	increased by 30% (5°C *versus* 26°C)	
	Duration of each huddle	increased by 31% (5°C *versus* 26°C) increased by 13% (5°C *versus* 26°C)	
Japanese macaque *Macaca fuscata*	Average number of mice per huddle Group size	increased by 66% (winter: 2.8°C *versus* autumn: 10.6°C)	Takahashi (1997)
Common bushtit *Psaltriparus minimus*	Roosting aggregation	no aggregation at 2.3°C clumping at −2.2°C	Smith (1972)
King penguin *Aptenodytes patagonicus*	Number of crèches	lower with "cold*wind*rain"	Le Bohec *et al.* (2005)
	Crèche size	higher with "cold*wind*rain"	
	Distance between chicks	lower with "cold"	
Emperor penguin *Aptenodytes forsteri*	Loose huddling formation	enhanced with lower temperatures (by 1.8°C) and higher winds (by 1.1m.s^{-1})	Gilbert *et al.* (2008*b*)
	Tight huddling formation	enhanced with lower temperatures (by 2.3°C) and higher winds (by 0.9m.s^{-1})	
	Huddling probability threshold of 90%	for climatic conditions of −25°C and 5 m.s^{-1} or −11°C and 15 m.s^{-1}	
	Tight huddling probability threshold of 50%	for climatic conditions of -22°C to −24°C	
	Group density	twofold increase at −23°C *versus* −10°C	

particularly adverse meteorological conditions. Similarly, it was shown that house sparrows (*Passer domesticus*) lower their inter-individual distance and increase the time spent in contact when ambient temperatures are reduced (Beal, 1978). Evans (1984) studied the crèching behaviour of young white pelicans (*Pelecanus erythrorhynchos*) and reported that adverse weather conditions increase the density of crèches, but not the occurrence of crèche formation. Unusually, Davis (1982) found no variation in the crèching behaviour of Adélie penguin (*Pygoscelis adeliae*) chicks with weather conditions during the Antarctic summer, although the author noted that meteorological conditions may not have been severe enough to induce such changes. Indeed, Gilbert *et al.* (2008*b*), studying the complex huddling behaviour of emperor penguins (*Aptenodytes forsteri*) throughout the Antarctic winter, showed that the occurrence of huddling increased at lower ambient temperatures and higher wind speeds, whereas huddling intensity was increased in response to lower ambient temperatures alone. Overall density of huddles was negatively correlated with ambient temperature, while group movements were linked to wind direction. It is also known that pinnipeds form large groups on land where animals are positively thigmotactic, and that this behaviour is associated with thermoregulation. For example, hundreds of walruses (*Odobenus rosmarus*) aggregate in densely packed herds during cold conditions or stormy weather (Miller, 1976; Riedman, 1990), particularly during the pupping season, when the young calves are susceptible to heat loss. Moreover, harbor seals (*Phoca vitulina*) appear to derive thermoregulatory benefits from grouping: as wind speed increased, the distances between individual seals in a group tended to decrease (Riedman, 1990).

Cold may not be the only determinant of huddling. A food shortage also favours energy conservation measures, and during the winter cold and food shortage may be linked. For example, grey mouse lemurs (*Microcebus murinus*) gather in

sleeping nests during the cold and dry season in which food is scarce (Perret, 1998); it is suggested that they use social thermoregulation to save energy that is reallocated to allow them to increase their body mass, even in a period of food restriction, in preparation for the subsequent reproductive season.

(b) Social factors

Sociality is a dominant factor promoting huddling. Many social rodents that huddle (Table 1) live in relatively large family groups, and huddle with close relatives. However, other social species may huddle with non-related individuals, and some solitary species occasionally become social and huddle in common nesting and roosting sites.

Social thermoregulation is a cooperative behaviour promoting benefits for each individual. As a result of kin selection, and linked to the high sociality of huddling individuals, most species huddle with close relatives. This is particularly obvious for pups huddling in a litter such as mice, rats, rabbits, or hamsters (*e.g.* Stanier, 1975; Alberts, 1978*a*; Sokoloff & Blumberg, 2002; Sokoloff *et al.*, 2002; Bautista *et al.*, 2003). Moreover, many rodents breed communally and use communal nesting during the reproductive season, favouring huddling with relatives (see Hayes, 2000 for review). Alpine marmots (*Marmota marmota*) also huddle within family groups of up to 20 individuals consisting of a territorial pair and mostly their own offspring (Arnold, 1990). Studies investigating sensory cues involved in huddling, especially on altricial newborns, reported the importance of thermal and olfactory cues (Alberts, 1978*b*; Sokoloff & Blumberg, 2001, 2002; Sokoloff *et al.*, 2002; Alberts, 2007). Alberts (2007), summarizing research on rat pups (*Rattus norvegicus*), reported changes in the sensory control of huddling during the first two weeks of postnatal life. Huddling behaviour is initially controlled by thermal cues ("physiological huddling"), a period during which endothermy prompts pups to aggregate (Sokoloff & Blumberg, 2002; Sokoloff *et al.*, 2002). At 15 days old, huddling of rat pups becomes dominated by olfactory stimuli ("filial huddling"; Alberts, 1978*b*; Brunjes & Alberts, 1979). As demonstrated in rat pups, sociality and kin recognition clearly plays a role in the formation of huddles.

However, huddles of some species consist of groups of non-relatives. For example, raccoons (*Procyon lotor*, Mech & Turkowsky, 1967) were observed nesting and huddling in the same burrow in a group of 23 individuals. A huddling group of more than 12 non-related deer mice (*Peromyscus maniculatus*) was described by Howard (1949). Golden-brown mouse lemurs (*Microcebus ravelobensis*) were observed gathered in sleeping nests during the dry and cold season, in groups of about four non-related individuals (Radespiel, Ehresmann & Zimmermann, 2003). Similarly, grey partridges (*Perdix perdix*), subjected to ambient temperatures below −30°C, were observed to huddle in groups of more than 20 non-related individuals in open sleeping sites (Putaala, Hohtola & Hissa, 1995). Huddles of emperor penguins and crèches of king penguin chicks (*Aptenodytes patagonicus*) generally involve thousands of non-related birds, which cooperate to share warmth during the Antarctic and subantarctic winters (Prévost, 1961; Ancel *et al.*, 1997; Le Bohec *et al.*, 2005; Gilbert *et al.*, 2006). Harbor seals (*Phoca vitulina*) also tend to haul out in groups of varying size and mixed age and sex classes, although females, dependent pups, and weaned pups sometimes form groups that are segregated from other animals (Riedman, 1990). Walruses (*Odobenus rosmarus*), one of the most positively thigmotactic of the pinnipeds, usually rest in large and dense groups involving unrelated individuals. Females and calves prefer to position themselves in the more crowded portion of the herd, and the calves often rest on top of the group (Riedman, 1990). During the nonbreeding season, Australian sea lions (*Arctocephalus pusillus*) gather in small groups that include all ages and both sexes, although only one adult male is usually present. More rarely, individuals belonging to different species are described huddling together. Meservey & Kraus (1976) reported the grouping of three different swallow species (*Iridoprocne bicolour, Hirundo rustica, Petrochelidon pyrrhonota*) during particularly low ambient temperatures.

For solitary species, a reduction in aggressiveness outside their reproductive period often favours grouping. This is the case for solitary rodents in winter, such as voles or mice (West & Dublin, 1984). Golden mice (*Ochrotomys nuttalli*) usually form mixed-sex groups in winter, whereas they are solitary in summer (Springer, Gregory & Barrett, 1981). Similarly, mouse lemurs (*Microcebus murinus, Microcebus ravelobensis*) are solitary during the reproductive season, but form groups in resting sites during the cold and dry season (Perret, 1998; Radespiel *et al.*, 2003). In the brush-tailed phascogale (*Phascogale tapoatafa*), a solitary marsupial, nest sharing between males and females was associated with an unusual period of low food availability and declining temperatures (Rhind, 2003).

(c) Morphological factors

Several morphological factors promote huddling. Small species with a high surface-area-to-volume ratio experience relatively greater heat loss, and represent the majority of species using huddling (*e.g.* many small rodents: Table 1). In addition, species or life stages with a high thermal conductance (poor insulation) will suffer a high rate of heat loss relative to the metabolic heat they produce. This is the case for altricial newborn mammals or birds, which are naked at birth or hatching and for which huddling represents an important strategy (*e.g.* rats, mice, rabbits, hamsters; Alberts, 1978*a*; Wang *et al.*, 1985; Sokoloff & Blumberg, 2002; Sokoloff *et al.*, 2002; Bautista *et al.*, 2003). Huddling is also critical for a unique mammal species, the naked mole rat (*Heterocephalus glaber*). These furless rodents live exclusively in subterranean burrows, and use huddling to regulate their body temperature in response to fluctuations in ambient temperature (Yahav & Buffenstein, 1991). Huddling is rarely used by large mammals or birds, which possess a lower surface-area-to-volume ratio. However, some large animals may use huddling when submitted to extreme conditions, such as emperor penguins (*Aptenodytes forsteri*). Huddling is used during moulting by pinnipeds, as during this

energetically demanding period the insulative properties of their fur are compromised; southern elephant seals (*Mirounga leonina*), for example, form tight groups during their moult (Riedman, 1990).

(3) General benefits and costs of huddling

Huddling can be considered as an adaptive behaviour, an energy conservation strategy that will enhance survival during cold conditions and thus also enhance an individual's fitness (Contreras, 1984; Canals, Rosenmann & Bozinovic, 1989; Canals *et al.*, 1998). Vickery & Millar (1984) designed a model encompassing the energetic advantages and disadvantages of huddling, with the hypothesis that huddling will occur when the benefits exceed the costs. Their model includes thermoregulatory variables such as ambient temperature, body temperature, temperature under shelter, and the reduction in exposed surface area while huddling. It also accounts for other energetic benefits and costs linked to huddling: the metabolic cost of being active, local food depletion resulting from the addition of animals to a huddle, feeding strategy, and the animal's time budget. In a general view, the benefits and costs of huddling are likely to be similar to the benefits and costs of any group membership. Benefits imply a decreased probability of predation (increased anti-predator vigilance, dilution of risk, predator confusion), improved foraging efficiency, and enhanced likelihood of finding a mate. Costs to group formation include increased probability of attacks by predators (a group being less cryptic than isolated individuals), competition while foraging, and potentially misdirected parental care (see Krause & Ruxton, 2002).

(a) Benefits

The main direct benefit of huddling is thermoregulatory. Vickery & Millar (1984) concluded from testing their model on small New World rodents *Peromyscus* spp. (deer mice), that huddling will have energetic advantages, and thus will be selected for, when ambient and nest temperature are well below the thermoneutral zone and when the animal spends most of its time in the nest. The thermoregulatory benefits of huddling, and their contributing factors, are discussed in detail in Section III.

Other indirect benefits occur, mainly linked to the fact that huddling animals are grouped. One non-metabolic benefit of huddling may be a decreased risk of predation, through a dilution effect (Calf, Adams & Slotow, 2002). A central position within the group would confer greater protection, as suggested for young jungle babblers (*Turdoides striatus*) that roost in the centre of the group (Gaston, 1977). Furthermore, participation in a group favours earlier detection of a predator, sentinel individuals being able to alert the rest of the group. In addition, close physical contact afforded by huddling facilitates a quicker reaction of the entire group in response to predators (Noske, 1985).

There may be a social function to huddling: close grouping could facilitate social harmony and structure social interactions between individuals. Kunkel (1974) suggested for tropical birds that clumping (or huddling) functions similarly to allopreening in the maintenance of the pair bond. In Japanese macaques (*Macaca fuscata*), Takahashi (1997) suggested that huddling strengthens social affiliations between non-related individuals. Affiliated dyads of Tibetan macaques (*Macaca thibetana*) that frequently groomed in the daytime, formed dyadic huddles in nightime huddling groups (Ogawa & Takahashi, 2003).

(b) Costs

There may be disadvantages to huddling: each addition of an animal to a huddle will increase the time and/or distance spent foraging by that group, unless food is superabundant or the animals are fasting (Vickery & Millar, 1984). Increased foraging time, which may be associated with a decrease in food quality, will make the animal's energy balance more negative. However, time spent foraging depends on feeding tactics: cooperative feeding within a group may result in a decrease in the time spent foraging. The costs of huddling due to food depletion will vary with food requirements, food availability, predator density and other environmental factors (Vickery & Millar, 1984). Cost of huddling also depends on the animal's time budget: an important factor in the model of Vickery & Millar (1984) used for deer mice, (*Peromyscus* spp.) is the ratio between the time spent in the nest and the time spent outside the nest. Huddling would become advantageous when animals seek shelter for long periods, especially in winter when low ambient temperatures and food scarcity favour inactivity.

Although not considered by Vickery & Millar (1984), a cost associated with huddling in dense groups may be the spread of pathogens and/or parasites. This cost is not easy to model, although it is well established as a cost associated with grouping and sociality (Krause & Ruxton, 2002).

III. FACTORS CONTRIBUTING TO HUDDLING ENERGY CONSERVATION

Huddling allows a reduction in the body surface exposed to cold and provides local heating of the surrounding environment. In addition to these two physical processes, other processes contribute to energy conservation. Canals *et al.* (1989) showed that the reduction in metabolic rate in huddling rodents is not a linear function of reduced heat loss. Physiological processes can make a contribution, notably adjustments in body temperature, and possibly also psycho-physiological factors.

(1) Physical processes

(a) Reduced body surface area exposed to cold

Huddling is used by mammals and birds to reduce heat loss, notably through a reduction in their cold-exposed body surfaces. This reduction in heat loss therefore allows a reduction in metabolic rate. Canals (1998) estimated that the

reduction in cold-exposed body surface area for huddling rodents ranges from 29 to 39%. Vickery & Millar (1984) estimated a value of 21% for mice (*Peromyscus maniculatus* and *Peromyscus leucopus*) huddling in groups of two, similar to the values of 29% (*P. leucopus* in groups of two) and 31% (groups of three) from Glaser & Lustick (1975). Pearson (1960) estimated a 28% reduction in cold-exposed body surface area for harvest mice (*Reithrodontomys megalotis*) huddling in groups of three, and Springer *et al.* (1981) calculated a 23% reduction for a group of three golden mice (*Ochrotomys nuttalli*). Interestingly, the estimated reduction in cold-exposed body surface area for a large bird such as the emperor penguin (*Aptenodytes forsteri*) is 74% when the birds are closely packed (Gilbert *et al.*, 2008a).

A reduction in cold-exposed body surface area is the primary reason used to explain the lower metabolic rates of huddling animals (Contreras, 1984; Canals, Rosenmann & Bozinovic, 1997; Canals *et al.*, 1998). Canals *et al.* (1997) estimated that it explained 58–94% of the energy savings associated with huddling, depending on the number of individuals involved and on group density. Gilbert *et al.* (2008a) estimated that about two-thirds of a 38% reduction in metabolic rate for free-ranging birds able to huddle was due to a reduction in cold-exposed body surface area, the exposure to warmer temperatures within the group accounting for the other third. However, Hayes *et al.* (1992) concluded in their study of short-tailed field voles (*Microtus agrestis*) that about 45% of the energetic benefits due to huddling at ambient temperatures of 0°C were due to a reduction in cold-exposed body surface area suggesting that local heating made the major contribution.

(b) Warming of local microclimate

When animals huddle, the ambient temperature surrounding each individual increases due to the combined heat loss of all the animals and therefore the temperature gradient between the local environment and the body is reduced. Huddling thus allows individuals to experience ambient temperatures closer to or within their thermoneutral zone. A 5°C increase in ambient temperature within the nest of huddling short-tailed field voles (*Microtus agrestis*) accounts for 55% of the energetic benefits of huddling (Hayes *et al.*, 1992). Huddling will also ameliorate the effects of wind cooling on the temperature gradient between the local environment and the animal in exposed species such as the emperor penguin (*Aptenodytes forsteri*). Emperor penguins within even a loosely structured group achieve average energy savings of 32% simply by sheltering themselves from the effect of wind-chill (Gilbert *et al.*, 2008a). Glaser & Lustick (1975) showed that Northern white-footed mice (*Peromyscus leucopus noveboracensis*) exposed to an ambient temperature of 5°C, when grouped in an open nest can reduce their metabolic rate by 29%. This reduced energy expenditure is similar to that measured for isolated mice exposed to an ambient temperature of 20°C. Indeed the nest temperature in the former group was 18°C. Similarly, Bautista *et al.* (2003) showed that the ambient temperature in the immediate vicinity of groups of

four to six huddling rabbit pups (*Oryctolagus cuniculus*) was 26°C, significantly higher than for groups of two (24°C) or for isolated pups (23°C). Willis & Brigham (2007) showed that the presence of cavity-dwelling big brown bats (*Eptesicus fuscus*) increased roost temperature by 7°C, and that there was a positive correlation between energy savings, the number of bats occupying a roost, and the maximum daily temperature in the roost. Moreover, they calculated that an individual roosting alone in a cavity would save 9% of its daily energy budget, whereas energy savings would account for 53% of its daily energy budget when roosting in a group of 45 bats. They suggested that social thermoregulation is a key factor motivating big brown bats to select large-volume tree cavities as roosts.

(2) Physiological processes

A third mechanism explaining energy savings relies on adjustments in body temperature of huddling animals (Vickery & Millar, 1984). Most huddling mammals and birds maintain a higher and more constant body temperature than their isolated counterparts, suggesting that huddling functions as a warming mechanism, presumably due to the reduction in heat loss (see Section IV.7). However, some species are known to lower their body temperature during huddling bouts, thus allowing them to maximize their energy savings through a further reduction in metabolic heat production. Great snow geese goslings (*Chen caerulescens atlantica*) reduced their body temperature by 0.8°C during huddling episodes (Fortin *et al.*, 2000) leading these authors to describe huddling as a mechanism to save energy through a lowering of body temperature. Similarly, white-footed mice (*Peromyscus leucopus*) exposed to ambient temperatures of 13°C in groups of three enter daily torpor and reduce their energy expenditure by 58% compared with isolated individuals, which do not enter torpor (Vogt & Lynch, 1982). Gray mouse lemurs (*Microcebus murinus*) also use daily torpor as an energy-saving strategy during the non-breeding season, and can be found resting in small groups in their nest (Perret, 1998; Séguy & Perret, 2005; Giroud *et al.*, 2008). Exposed to low ambient temperatures and under a calorie-restricted diet, males placed in groups of two show an increased duration of torpor, but a similar torpor depth, compared with isolated males (Séguy & Perret, 2005). Moreover, during both breeding and non-breeding seasons, metabolic rate was minimal when three or four individuals shared the same nest, suggesting that nest-sharing in this solitary primate is an important strategy to save energy and cope with seasonal food shortage (Perret, 1998). Roverud & Chappell (1991) monitored the body temperature of lesser bulldog bats (*Noctilio albiventris*) placed in groups of one, two, three, four, eight, and 16 individuals at three ambient temperatures (10°C, 20°C and 30°C). At 10°C and 20°C, individuals placed in groups of four or more showed a more variable body temperature, and a greater tendency to exhibit low body temperatures. The minimum body temperature measured in groups of one to three was 32.3°C, whereas body temperatures of 27.4°C were measured in

larger groups. Roverud & Chappell (1991) concluded that huddling would allow the animals to decrease their metabolic rate by becoming hypothermic. They suggested a link with predation: solitary hypothermic individuals would be more vulnerable to predation (minimum body temperature for flight is 35°C), while animals benefiting from the protection of a group could lower their body temperature.

Several studies (Prévost, 1961; Prévost & Sapin-Jaloustre, 1964; Mougin, 1966) on emperor penguins (*Aptenodytes forsteri*) showed that free-ranging individuals, free to huddle, maintain a rectal temperature (35.5°C) that is 1.1°C lower than loosely grouped birds (36.6°C; restrained in groups of 5–10 individuals), and 2.2°C lower than isolated individuals (37.7°C) exposed to the same environmental conditions. Gilbert *et al.* (2007*b*) showed that free-ranging emperor penguins adjust their body temperature during their breeding cycle: it is reduced during pairing from 37.5°C (mid-pairing) to 36.5°C (end of pairing), and maintained during a successful incubation at 36.9°C. Core temperatures while huddling during pairing decreased significantly by 0.5°C; no such decrease was observed during a successful incubation. However, in cases of egg loss, body temperatures were adjusted to 35.5°C, with a further reduction of 0.9°C during huddling. These results suggest a trade-off between the demands of successful egg incubation and energy savings. A possible explanation for the slight decrease or the constancy in core temperature inside dense huddles is that the emperor penguins' metabolic rate is depressed in response to the reduction in their cold-exposed body surfaces, thus permitting them to save energy (Gilbert *et al.*, 2007*b*). Gilbert *et al.* (2008*a*) estimated from previous measurements of metabolic rate associated with different body temperatures (Le Maho, Delclitte & Chatonnet, 1976; Pinshow *et al.*, 1976), that a core temperature decline of 1°C between 37.7°C (active body temperature; Le Maho *et al.*, 1976; Pinshow *et al.*, 1976) and 36.7°C (observed during the breeding cycle) would represent for emperor penguins a metabolic reduction of 17%. Gilbert *et al.* (2008*a*) therefore hypothesize that huddling free-ranging birds are able to maintain a lower body temperature compared with loosely grouped birds that are unable to huddle, because a decline in metabolic heat production for loosely grouped birds would lead to body cooling, which would be highly disadvantageous for incubation. These authors suggest that the energy savings of huddling birds are due to metabolic depression allowing them to incubate successfully while enduring a four-month fast.

(3) Psycho-physiological processes

In addition to these physiological processes, it has been suggested that the metabolic reduction observed in social huddling animals is influenced by chemically mediated effects between related individuals in close contact. Martin *et al.* (1980) compared the oxygen consumption of mice (*Mus musculus*) and Mongolian gerbils (*Meriones unguiculatus*) grouped in huddled trios, separated trios (animals tested simultaneously but prevented from physical contact) and isolated individuals, at ambient temperatures of 10°C, 15°

and 20°C. The rates of increase of oxygen consumption as a function of the decrease in ambient temperature did not differ significantly between huddled and separated trios, but were higher in isolated individuals. The authors suggested that significant energy savings can occur without contact, and that other cues from conspecifics (sight, sound, smell, body heat) participate in reducing metabolic rate. However, Contreras (1984) found opposite results using the same protocol, with huddled, separated trios, and isolated individuals of the same species, at ambient temperatures of 5°C, 12°C, and 20°C. This author found that the energy expenditure of separated trios was higher than huddled trios, and did not support a psycho-physiological component to a reduction in metabolic rate of huddled animals, but concluded that energy savings were mainly due to the reduction in the cold-exposed body surfaces permitted by grouping.

IV. HUDDLING ENERGETICS

Many studies have attempted, using both indirect and direct methods, to quantify the energetic benefits of huddling. Early studies focused on the benefits of group membership on survival rates, and the effects on body heat conservation at low ambient temperatures. Other studies compared the food intake and mass loss of grouped and isolated individuals as an index of metabolic energy expenditure. Some researchers compared growth rates of huddling newborn mammals to isolated animals. Recent techniques which can quantify more precisely the energetic benefits associated with huddling have allowed more detailed investigations into the metabolic rates of huddled individuals.

(1) Increased survival rates at low temperatures

Huddling may be one of the key factors allowing the colonisation of particularly cold habitats by endotherms: the most extreme example being the emperor penguin, which breeds during the Antarctic winter, enduring a four-month fast to incubate its egg (Prévost, 1961; Ancel *et al.*, 1997; Gilbert *et al.*, 2008*a*). Gerstell (1939) demonstrated that huddling is an important factor contributing to survival rates of bobwhite quails (*Colinus virginianus*) at low ambient temperatures. Similarly, survival rates of domestic mice (*Mus musculus*) in groups of two or five, exposed to low ambient temperatures (+4°C and −3°C) are higher than those of isolated mice exposed to the same conditions (Prychodko, 1958). Newborn rabbits (*Oryctolagus cuniculus*) in groups of two, four, five or six and exposed to temperatures of 17–22°C have higher survival rates than isolated newborns: six of 10 isolated pups died between day 3 and day 7, whereas no grouped pup died (Bautista *et al.*, 2003). Grouped deer and white-footed mice (*Peromyscus* spp.) exposed to temperatures of −23°C, corresponding to a lethal thermal stress, survive for longer than isolated individuals (Fig. 2; Sealander, 1952). Brenner (1965) reported increased survival rates of grouped common starlings (*Sturnus vulgaris*), exposed to ambient
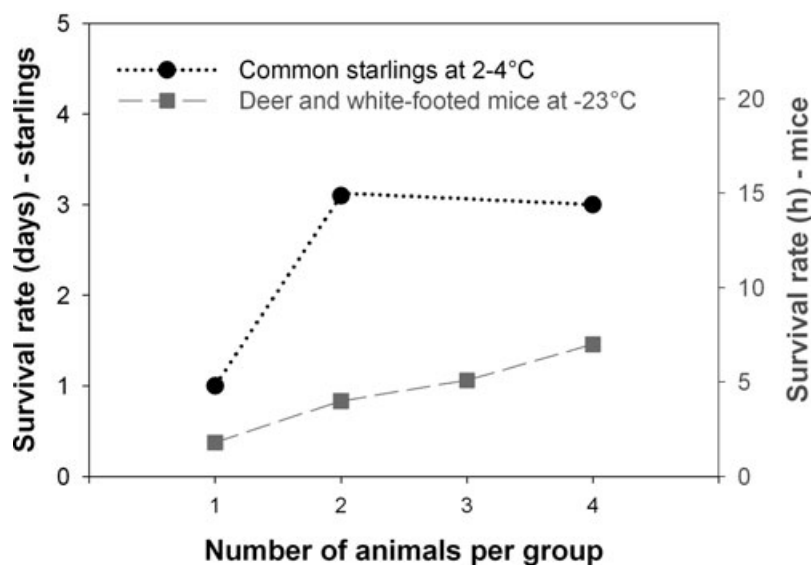
Fig. 2. Means ± S.D. survival rates of common starlings (*Sturnus vulgaris*; Brenner, 1965) and deer and white-footed mice (*Peromyscus* spp.; Sealander, 1952) exposed to 2–4°C and −23°C, respectively, as a function of the number of animals per group.

temperatures between 2 and 4°C (Fig. 2), linking the increase in survival to a reduced metabolic rate.

(2) Reduced food intake

Due to the reduced cost of thermoregulation, huddling lowers food intake and therefore can enhance survival under conditions of food shortage. Domestic mice (*Mus musculus*) caged in groups of five and two at ambient temperatures of +25°C, +4°C and −3°C consume significantly less energy than isolated mice (Fig. 3; Prychodko, 1958). Indeed, the food consumption of two mice kept together at −3°C is the same as the value for one mouse kept alone at +5.5°C (Prychodko, 1958). Springer *et al.* (1981) showed that food intake of isolated golden mice (*Ochrotomys nuttalli*) is 22% greater compared to golden mice in a group of
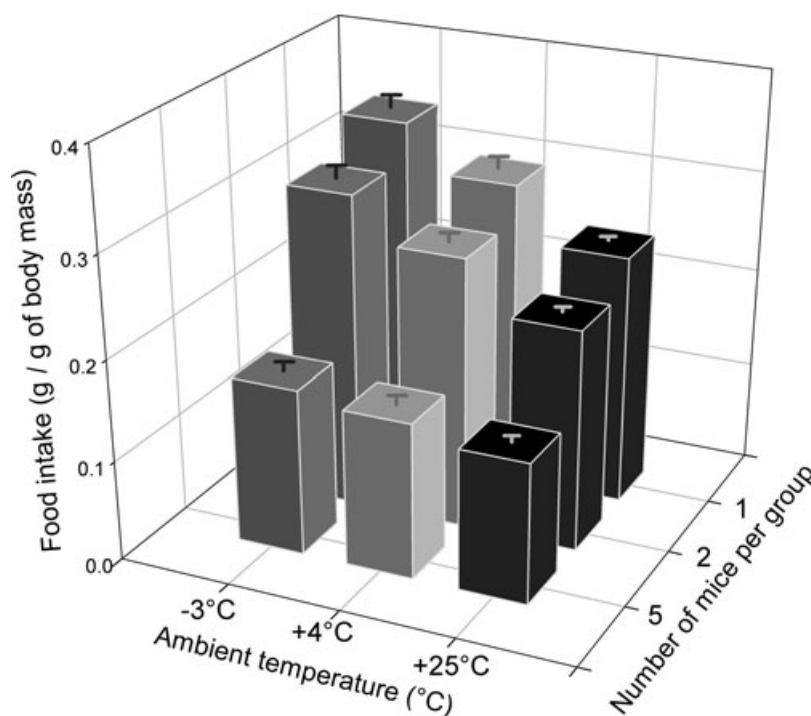

Fig. 3. Mean + S.E.M. food intake (g/g of body mass) of house mice (*Mus musculus*) placed isolated or in groups of two or five individuals, exposed to ambient temperatures of −3°C, +4°C, and +25°C (Prychodko, 1958).

three at $22°C$ (0.50 *versus* 0.41 kcal g^{-1} day^{-1}, respectively). Although all mice received the same diet, those living in grouped conditions ingested less, suggesting that they required less energy than those kept individually (Springer *et al.*, 1981). Kauffman *et al.* (2003) showed that Siberian hamsters (*Phodopus sungorus*) raised in groups of three and exposed to ambient temperatures of $5°C$, consume 16% less food that isolated hamsters.

(3) Decreased body mass loss

Huddling can permit individuals to decrease their body mass loss, which may be of particular importance during an adverse period. Male emperor penguins (*Aptenodytes forsteri*) have to fast for four months in order to breed successfully, and thus must exploit their limited body reserves optimally (Prévost, 1961; Ancel *et al.*, 1997; Gilbert *et al.*, 2008a). Daily body mass loss has been measured in enclosed, isolated and loosely grouped birds, and in unrestrained free-ranging birds (Prévost, 1961; Prévost & Sapin-Jaloustre, 1964; Ancel *et al.*, 1997). On average, free-ranging and loosely grouped emperor penguins lose 132 and 178 g day^{-1}, respectively, representing a 26% reduction in daily body mass loss for free-ranging birds compared to the loosely grouped birds (Gilbert *et al.*, 2008a). Moreover, daily body mass loss in loosely grouped birds is on average 40% lower than in isolated birds (299 g day^{-1}). Therefore the overall reduction in daily body mass loss between isolated and free-ranging birds can be as high as 56% (Gilbert *et al.*, 2008a). In bats, Howell (1976) showed that individuals of Pallas's long-tongued bat (*Glossophaga soricina*) maintained in clusters of eight at $25-28°C$ experience a body mass loss over their diurnal resting period corresponding to 5.5% of their total body mass, while isolated individuals lose 18.3% of their total body mass; huddling enables a 70% reduction in body mass loss. For some other species of bats (*Myotis* spp.), exposed to ambient temperatures ranging from $17°C$ to $27°C$ in their natural habitat, Studier, Procter & Howell (1970) demonstrated that isolated individuals underwent a body mass loss of $6-22%$ of their initial body mass over their diurnal resting period, whereas individuals in groups of four lost $10-16%$ of their initial body mass. A reduction in body mass loss due to huddling was especially evident for fringed myotis (*Myotis thysanodes*), which lost 21% of its body mass when isolated compared to 14.5% when in groups of four, corresponding to a 31% lowering in body mass loss. In deer mice (*Peromyscus* spp.) exposed to ambient temperatures of $-23°C$ in groups of two and four, Sealander (1952) found a body mass loss 39% and 59% lower, respectively, compared with isolated individuals.

(4) Increased growth

Huddling allows newborn altricial mammals to reduce loss of energy as heat and thereby increase their growth rate (mice: Stanier, 1975; rats: Alberts, 1978a; Cape porcupines *Hystrix africaeaustralis*: Haim, Van Aarde & Skinner, 1992; rabbits: Bautista *et al.*, 2003; Gilbert *et al.*, 2007a). Benefits of huddling on growth rates are indeed particularly evident for newborns of altricial species, which huddle in the nest soon after birth. While many mammalian mothers spend long periods within the nest, feeding, cleaning, or rewarming their offspring, the European rabbit (*Oryctolagus cuniculus*) doe is an exception: she leaves the pups after birth, and only nurses them for $3-5$ min once a day (Zarrow, Denenberg & Anderson, 1965; Lincoln, 1974; Hudson & Distel, 1982). In order to investigate the energetic benefits of huddling in altricial newborns, Bautista *et al.* (2003) calculated an index of milk conversion efficiency per gram of body mass gained for rabbit pups in their first 10 days: isolated, in groups of two, and in groups of four to six. They showed that huddling benefits are particularly important for pups of two to five days old, at which stage they are thermoregulatorily inefficient, have no fur and a large surface area relative to body mass. The capacity to convert milk into body mass was significantly higher for pups in groups of four to six compared with isolated pups. Moreover, to investigate further how huddling promotes allocation of energy when animals are faced with conflicting demands for growth, Gilbert *et al.* (2007a) investigated changes in body composition, *i.e.* the relative proportions of fat-free mass and fat mass, of rabbit pups (*Oryctolagus cuniculus*) either isolated or placed in groups of two, four, and eight. Using the doubly labelled water technique, these authors showed that the benefits of huddling were linked to the thermoregulatory capacities of the pups: thermoregulatorily inefficient (from two to five days old) pups in a group of eight used 40% less energy for thermogenesis than did isolated pups, whereas thermoregulatorily efficient pups (from five to 10 days old) in a group of eight used 32% less energy. Huddling pups could channel the energy saved into processes of growth and they accrued fat (on average 4.5 g) whereas isolated pups lost 0.7 g of fat. Energy saved through huddling was thus reinvested into fat storage, and huddling can be seen as a behaviour necessary for an altricial mammal to reduce its thermoregulatory costs until it has acquired enough insulative fat mass and a more favourable surface-to-volume ratio (Gilbert *et al.*, 2007a).

(5) Reduced energy expenditure

As the major benefit of huddling is to save energy, many studies have investigated the metabolism of grouped and isolated individuals. Several methods can be used to estimate the metabolic rate of an animal. The most common is respirometry in which oxygen consumption and/or carbon dioxide production are measured over a defined period of time (Randall, Burggren & French, 2002). However, the respirometry method involves the confinement of animals in small cages that can bias energy budget data due to increased stress, or modification in their activity. Moreover, these studies often monitor metabolic rate for a time period of a few hours only (mostly $1-3$ h), which may not be representative of overall huddling benefits. However, this method is used widely with results available to our knowledge from 14 studies on mammals and five on birds (Table 3). From Table 3 short-term respirometry studies (R) on adult

Table 3. Metabolic savings (%) due to huddling in mammals and birds (highlighted in grey for comparison with Tables 1 and 2) for a range of group sizes compared to isolated individuals, except where indicated. Metabolic rate was measured by respirometry over several hours (R), respirometry over 24 h (R-24h: daily metabolic rate) or isotopic method (IM). Studies are ordered according to whether they are (1) below the thermoneutral zone (TNZ), species exposed to cold ambient temperatures in the laboratory or in their natural habitat, (2) close to or within the TNZ, and (3) over a wide range of temperatures including temperatures below and within the TNZ.

	Species	Group size	Metabolic savings (%) from huddling	Temperature (°C)	Method	Reference
	Below thermoneutral zone					
ADULTS	African four-striped grass mice *Rhabdomys pumilio*	reduced by one-half	16	various temperatures	IM	Scantlebury *et al.* (2006)
	Bank vole *Clethrionomys glareolus*	2, 4	13	various temperatures	R-24h	Gorecki (1968)
	Emperor penguin *Aptenodytes forsteri*	Free-ranging	16 (compared to loosely-grouped)	winter ambient temperature	IM	Ancel et al. (1997)
	Antelope ground squirrel *Ammospermophilus leucurus*	3	40	winter ambient temperature	IM	Karasov (1983)
	Grey partridge *Perdix perdix*	3, 6, 9	6, 13, 24	−30	R	Putaala *et al.* (1995)
	Muskrat *Ondrata zibethicus*	4	11 and 14	−10 and 0	R	Bazin & MacArthur (1992)
	Harvest mouse *Reithrodontomys megalotis*	3	28	1	R	Pearson (1960)
	Green woodhoopoe *Phoeniculus purpureus*	4	30	5	R	Du Plessis & Williams (1994)
	White-backed mousebird *Colius colius*	6	50	15	R	McKechnie & Lovegrove (2001)
	Close to or within thermoneutral zone					
	Townsend's vole *Microtus townsendii*	4	16	19	R-24h	Andrews *et al.* (1987)
	European common vole *Microtus arvalis*	6–9	36	20	R	Trojan & Wojciechowska (1968)
	Striped field mouse *Apodemus agrarius*	2, 3	17, 29	20	R-24h	Gorecki (1969)
	Tundra vole *Microtus oeconomus*	2, 3	10, 15	20	R	Gebczynska (1970)
	Common bushtit *Psaltriparus minimus*	2	21	20	R	Chaplin (1982)
	Gray mouse lemur *Microcebus murinus*	2, 3	20, 40	24–26	R	Perret (1998)
	Australian hopping mouse *Notomys alexis*	4	18	28	R	Baudinette (1972)
	Naked mole rat *Heterocephalus glaber*	8	22	32	R	Yahav & Buffenstein (1991)
NEWBORNS & PUPS	Domestic rabbit *Oryctolagus cuniculus*	8	32–40	22	IM	Gilbert *et al.* (2007a)
	Rat *Rattus norvegicus*	8	34	29	R	Alberts (1978a)
	House mouse *Mus musculus*	isolated at 30°C *versus* 4 at 20°C	similar metabolic rate		R	Stanier (1975)
	Wide range of temperatures (below and within thermoneutral zone)					
ADULTS	House mouse *Mus musculus*	3	22, 14, 14	10, 15, 20	R	Martin *et al.* (1980)
	Yellow-necked field mouse *Apodemus flavicollis*	2, 3, 4, 5	13 to 44	5, 10, 15, 20, 25	R	Fedyk (1971)

ADULTS Bank vole C*lethrionomys glareolus*	2, 3, 5	8 to 35	5, 10, 15, 20, 25	R and R-24h	Gebczynski (1969)
Northern white-footed mouse *Peromyscus leucopus noveboracensis*	2	27 and 53	5 (no nest) and 18 (with nest)	R	Glaser & Lustick (1975)
Striped field mouse *Apodemus agrarius*	2, 3	12 to 21	5, 20	R-24h	Tertil (1972)
Lesser bulldog bat *Noctilio albiventris*	>4	38 and 47	10 and 20	R	Roverud & Chappell (1991)
Red-billed woodhoopoe *Phoeniculus purpureus*	5	29 and 12	10 and 20	R-24h	Boix-Hinzen & Lovegrove (1998)
Speckled mousebird *Colius striatus*	2, 4	11 to 31	<TNZ and 30–35	R	Brown & Foster (1992)

mammals exposed to ambient temperatures below or within their thermoneutral zone, and placed in groups from two to nine, show that huddling permits an average metabolic savings of $26 \pm 11\%$ (mean $\pm$ S.D., range 8–53%; Table 3). For birds, huddling decreases metabolic rate by $22 \pm 13\%$ (mean $\pm$ S.D., range 6–50%; Table 3). These energy savings depend on species, ambient temperature, and the number of grouped individuals.

Short-term metabolic rate measurements may result in imprecision in the evaluation of huddling energetics. For example, most species show a circadian activity pattern linked to variations in body temperature, which may influence energy calculations. Tertil (1972) showed that the metabolic rate of striped field mice (*Apodemus agrarius*) in groups of three, exposed to temperatures of 20°C was lowered by 18% during the daytime and by 9% during the night, compared to isolated individuals. It may be better, therefore to measure oxygen consumption over a period of at least 24 h, to obtain an average daily metabolic rate (R-24h, Table 3). To our knowledge five studies have determined the average daily metabolic rate of isolated and grouped rodents (Gorecki, 1968, 1969; Gebczynski, 1969; Andrews, Phillips & Makihara, 1987; Tertil, 1972) and one study is available on isolated and grouped birds (Boix-Hinzen & Lovegrove, 1998). These studies on adult mammals exposed to various ambient temperatures below or close to the species' thermoneutral zone, and placed in groups of two to four, show that huddling reduces metabolic rate by an average of $17 \pm 6\%$ (mean $\pm$ S.D., range 12–29%). This average is lower than the 26% calculated for short-term measurements, although the species examined, ambient temperatures and the number of individuals per group are not fully comparable. As an example, Gebczynski (1969) showed that the daily metabolic rate of bank voles (*Clethrionomys glareolus*) grouped by three and five, exposed to decreasing ambient temperatures from 25 to 14°C increased by 3.4 and 2.1% per °C, respectively, and exposed to decreasing ambient temperatures from 14 to 3°C increased by 1.8 and 1.6% per °C. These rates are lower (2.6 and 1.9% on average from 25 to 3°C) than for experiments using 1 h measurements, wherein for voles grouped by three and five and exposed to temperatures from 25 to 5°C, increases were of 3.4 and 2.5% per °C respectively (Gebczynski, 1969).

Respirometry measures the total energy expenditure of a group, which is then averaged to give individual values for comparison with isolated animals. Furthermore, it requires the use of respirometry chambers, which may modify natural behaviour and may require a period of habituation before energy expenditure can be measured. By contrast, the doubly labelled water technique generally uses stable isotopes (^{18}O and ^{2}H) to quantify total energy expenditure on unrestrained individual animals during their normal daily activities. Oxygen from the body water is known to be in isotopic equilibrium with the oxygen in exhaled carbon dioxide (Lifson & McClintock, 1966; Speakman, 1997). The difference between the elimination rate of oxygen and hydrogen of body water enriched with ^{18}O and ^{2}H then allows determination of carbon dioxide production, and thus energy expenditure, over relatively long periods (Lifson & McClintock, 1966). Nagy (1975) extended this method to measure the energy expenditure of free-living, undisturbed animals. Although this method has great potential for measuring the huddling energetics of undisturbed animals in their natural environment, it has not been widely used, probably due to the fact that it is costly and requires sophisticated analyses. To our knowledge, only four studies have used this type of method to estimate energy expenditure during huddling (Table 3), making it difficult to compare their results with other methods. However, the energy expenditure of free-living African four-striped grass mice (*Rhabdomys pumilio*) was increased by 19% when their natural group sizes were halved (Scantlebury *et al.*, 2006), while in winter antelope ground squirrel (*Ammospermophilus leucurus*) can decrease their energy expenditure by 40% by huddling in groups of three (Karasov, 1983; Table 3).

(6) Reduced water use

Huddling may also reduce water requirements for species in arid habitats or seasons. Naked mole rats (*Heterocephalus glaber*), subterranean rodents of the arid Eastern African deserts, are thermoregulatorily inefficient and possess no fur. When exposed to an ambient temperature within their thermoneutral zone, huddling individuals show both a 22% reduction in oxygen consumption and a 31% decrease in

evaporative water loss compared to isolated individuals (Yahav & Buffenstein, 1991). African four-striped grass mice (*Rhabdomys pumilio*), which are found in arid habitats as well as grasslands in southern Africa, also use huddling to decrease their water expenses. Scantlebury *et al.* (2006) showed that when groups of mice were halved in size their energy expenditure increased by 19% and their water turnover by 37%. They suggested that water conservation permitted by huddling may explain differences between the social structures of these mice in different habitats: they live in groups in arid habitats but are solitary in grasslands. Similarly, Baudinette (1972) showed that Australian hopping mice (*Notomys alexis*) huddling in groups of four at ambient temperatures of 28°C lost 25% less pulmocutaneous water than isolated individuals. In their arid Australian desert habitat, these mice use group nesting and fossoriality to cope with high temperatures and drought conditions (Baudinette, 1972).

(7) Maintenance of body temperature

Huddling can allow an animal to maintain its body temperature without increasing metabolic heat production (Vickery & Millar, 1984). As described in Section III.2, some species are known to lower their body temperature during huddling, allowing them to maximize their energy savings through a reduction in metabolic heat production. However, most huddling endotherms maintain a higher and more constant body temperature than their isolated counterparts, suggesting that huddling functions for them as a warming mechanism. This is of critical importance for small species, for which homeothermy is particularly costly, or during periods such as gestation, incubation or growth, where maintenance of a high body temperature can increase an individual's fitness.

Grouped red-billed woodhoopoes (*Phoeniculus pupureus*), exposed to ambient temperatures from 10°C to 30°C during their active period, have a body temperature 0.4°C greater than isolated individuals (41.4 *versus* 41.0°C) while during their resting period the body temperature of grouped birds is 0.8°C greater than in isolated individuals (38.6 *versus* 37.8°C) (Boix-Hinzen & Lovegrove, 1998). Similarly, the body temperature of common starlings (*Sturnus vulgaris*) in groups of four at ambient temperatures of 2–4°C is 1.9°C greater than in isolated birds (41.7 *versus* 39.8°C; Brenner, 1965). Huddling allows speckled mouse birds (*Colius striatus*) to reduce the amplitude of their body temperature variations (Brown & Foster, 1992). White-backed mouse birds (*Colius colius*) show hypothermic phases during their resting period, but huddling birds reduce these periods of hypothermia (McKechnie & Lovegrove, 2001). Among mammals, it has been shown that grouped Townsend's voles (*Microtus townsendii*) maintain higher body temperatures compared with isolated individuals: 40.0°C in groups of four individuals, 39.2°C in groups of two, and 38.6°C when isolated (Andrews *et al.*, 1987). In the same way, grouped and non-hibernating Pallas's long-tongued bats (*Glossophaga soricina*) maintain a higher and less variable body temperature (37.5°C) than

isolated bats (33.5°C) that use torpor as an energy-saving mechanism (Howell, 1976).

Huddling allows altricial newborn mammals to maintain their body temperature at an optimum for growth. Stanier (1975) showed that young mice (*Mus musculus*) of 5 g exposed to an ambient temperature of 20°C in groups of four maintain a body temperature of about 30°C, compared to 27°C when isolated. Grouped tuco-tucos (*Ctenomys talarum*), exposed to ambient temperatures of 19°C at two and six days old, despite thermoregulatory inefficiency, show less variation in body temperature than isolated individuals (Cutrera, Antinuchi & Busch, 2003). Brown adipose tissue of newborn dwarf Campbell's hamsters (*Phodopus campbelli*) is not functional before nine days old, and newborns are not able to thermoregulate independently before 15 days old. However, newborns aged six days show short episodes of thermogenesis, in contrast to isolated individuals that do not increase their body temperature independently before nine days of age (Newkirk, Silverman & Wynne-Edwards, 1995). Bautista *et al.* (2003) reported that newborn rabbits (*Oryctolagus cuniculus*), aged 2–5 days and placed in groups of four to six maintain on average a higher body temperature (36.5°C) than isolated pups (34.0°C). Similarly, Gilbert *et al.* (2007*a*) showed that thermoregulatorily inefficient rabbit pups (from two to five days old) in groups of four and eight had a significantly higher body temperature than pups in groups of two and one (37.8 *versus* 37.0°C, respectively). However, when able to thermoregulate independently, from six to 10 days old, no differences were noted. Female rabbits only visit their pups for a few minutes once a day for nursing. Both body temperature and physical activity of the pups increased significantly before as well as after suckling (Jilge, 1993, 1995; Jilge *et al.*, 2000; Gilbert *et al.*, 2007*a*). Such anticipatory behaviour may help them to be more competitive when suckling (Hudson & Distel, 1982; Distel & Hudson, 1984; Jilge *et al.*, 2000). Gilbert *et al.* (2007*a*) showed that huddling helps pups to raise their body temperature before suckling and allows them to be more competitive, compared with isolated pups. Similarly to newborn altricial mammals, naked mole rats (*Heterocephalus glaber*) are non-homeotherms even as adults. The body temperature of isolated individuals fluctuates in response to changes in ambient temperature, whereas they are able to maintain a relatively constant body temperature of 32–33°C when in groups of four. Huddling thus appears to be an important temperature-regulation behaviour in this eusocial species (Yahav & Buffenstein, 1991).

It has also been shown that huddling is involved in the regulation of hypothermic bouts of hibernating mammals. Alpine marmots (*Marmota marmota*), which hibernate within family groups, possess a higher body temperature when awake than during hibernation phases, and therefore contribute to warming their relatives during their waking phases (Arnold, 1988). Indeed, individuals entering a hibernating phase maintain a higher body temperature when huddled with awake individuals. Similarly, the duration of torpor phases in young yellow-bellied marmots (*Marmota*

flaviventris) is lower in groups of three than in single individuals (Armitage & Woods, 2003). Arnold (1993) suggested that huddling allows a reduction in energy costs for the rewarming phase following hibernation bouts. However, such energetic benefits may not be equally shared among all individuals within a group. Huddling would be particularly advantageous for juveniles with a lower body mass than adults (Arnold, 1988): for instance, group hibernation in alpine marmots would particularly help infants to rewarm (Arnold, 1990). However, a study on young yellow-bellied marmots does not support this suggestion: Armitage & Woods (2003) found that asynchronous bouts of torpor among young marmots increase their metabolic rate, offsetting one benefit of hibernating in groups.

V. VARIATION IN THE EFFECTIVENESS OF HUDDLING

Canals *et al.* (1998) proposed a general model explaining the reduction in metabolic rate for huddled animals as a function of the number of individuals in the group and of the individual capacity to change form and shape when grouped (deformation coefficient). This last variable, derived from a reduction in exposed body surface area during huddling, plays a major role in huddling effectiveness. The authors note that phylogeny indeed plays an important part in huddling effectiveness, which varies considerably more (18–60%) among genera than within a genus (0.3–6%). In addition, other factors contribute to variation in huddling effectiveness, including ambient temperature, huddling intensity, and developmental stage.

(1) Group size

Larger group sizes allow a greater reduction in the area of the body exposed to cold. A compilation of five studies on adult rodents exposed to various ambient temperatures and placed in groups of two to five individuals [*Clethrionomys glareolus* (Gebczynski, 1969), *Microtus oeconomus* (Gebczynska, 1970), *Apodemus flavicollis* (Fedyk, 1971), *Apodemus agrarius* (Tertil, 1972), *Mus musculus* (Martin *et al.*, 1980)] indicates clearly that the energetic benefits of huddling increase significantly as a function of group size (Fig. 4A). From the regression line shown, for temperatures from 5 to 25°C, huddling reduces mean ± S.D. energy expenditure by 16 ± 5% and 31 ± 13% for rodents in groups of two and five, respectively. In one of the studies included in Fig. 4, Fedyk (1971) reported a $3.6\%°C^{-1}$ reduction in energy expenditure in groups of two yellow-necked field mice (*Apodemus flavicollis*), while the reduction reached $7.9\%°C^{-1}$ for a group of five. In another study included in Fig. 4, Gebczynski (1969) measured a $5.6\%°C^{-1}$ increase in oxygen consumption for isolated bank voles (*Clethrionomys glareolus*), but only 3.2 and $2.5\%°C^{-1}$ for groups of two and five, respectively.

According to Contreras (1984), the reduction in exposed body surface area is proportional to the number of individuals within the group raised to the power -0.33. However, Canals *et al.* (1989) argue that there will be a critical number of huddling individuals above which any further reduction in cold-exposed body surface area would be negligible. According to this model, they predict that energy expenditure would be minimal in rodents for groups of five individuals. Indeed, the data shown in Fig. 4A appear to take a U-shaped form, suggesting that huddling energetic benefits are maximal for rodents in groups of four over at least the ambient temperatures 15, 20 and 25°C. Little extra benefit is gained for rodents placed in groups of five at 5 and 10°C. Similarly, Roverud & Chappell (1991) report that the energetic benefits of huddling in lesser bulldog bat (*Noctilio albiventris*) are linked to the number of individuals involved: increasing the group size beyond four individuals had little additional effect on the reduction in metabolism. Vickery & Millar (1984) note indeed that a group composed of too many individuals would not necessarily be advantageous, due to increasing competition among individuals, which would force more individuals to occupy the periphery of the group. Kotze, Bennett & Scantlebury (2008) report that both Damalarand mole rats (*Cryptomys damarensis*) and Natal mole rats (*Cryptomys hottentotus natalensis*) save more energy in larger groups as opposed to smaller groups. However, Damalarand mole rats showed a higher decrease in oxygen consumption with increasing group size compared to Natal mole rats, suggesting that the optimal number of individuals within a group varies among species (linked to the social capacities for aggregation, the deformation coefficient of individuals and ambient temperature).

(2) Ambient temperature

Most authors agree that ambient temperature has a role in the energy benefits of huddling, although the exact effect is not yet clear. It does appear to be linked to the species' lower critical temperature and the number of individuals involved in huddling. Canals *et al.* (1998) suggested that close to the lower limit of an animal's thermoneutral zone (*i.e.* for temperatures ranging from 5°C below the lower critical temperature to the lower critical temperature), the effectiveness of huddling will be linked to the intensity of grouping of individuals within the huddle: closer groupings facilitating increased effectiveness through a greater reduction in cold-exposed body surface area. Below this limit (more than 5°C below the lower critical temperature), the benefits of huddling increase as ambient temperature declines, independent of the intensity of huddling. However, the model of Vickery & Millar (1984) predicts only a minor role for ambient temperature in determining group formation, until environmental temperature approaches the lower critical temperature. Martin *et al.* (1980) note that "the point at which the energetics of huddled and isolated animals equilibrate differs between species, but generally extrapolates near their lower limit of thermoneutrality". Other studies have shown the energetic benefits of huddling (Gorecki, 1968; Gebczynska & Gebczynski, 1971; Contreras, 1984) and its effectiveness (Canals *et al.*, 1998) to decrease at high ambient
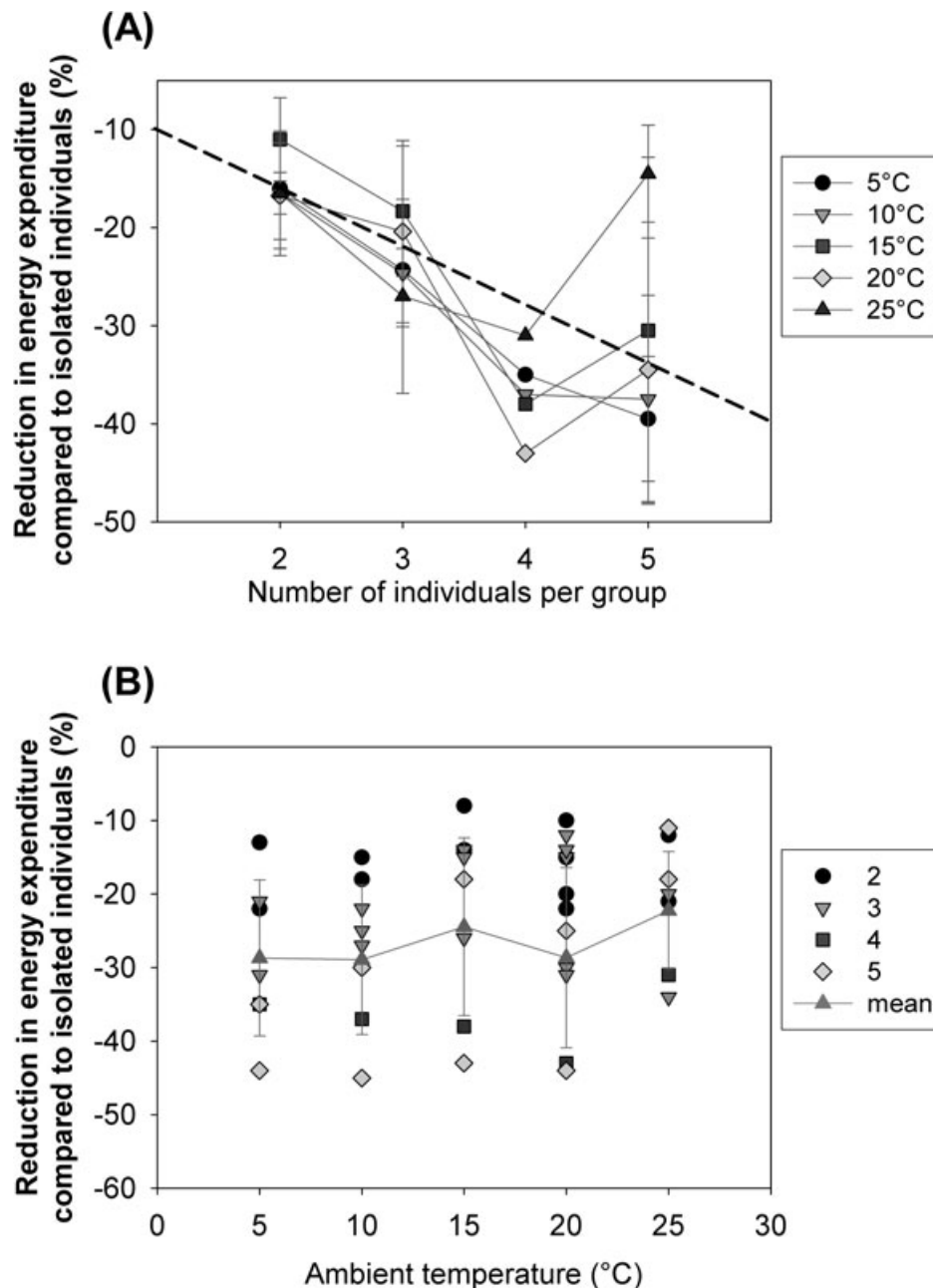
Fig. 4. (A) Reduction in energy expenditure due to huddling (%) at various ambient temperatures (from 5°C to 25°C) of grouped animals compared to isolated individuals [data are from Gebczynska (1970) for *Microtus oeconomus*, Martin *et al.* (1980) for *Mus musculus*, Fedyk (1971) for *Apodemus flavicollis*, Gebczynski (1969) for *Clethrionomys glareolus*, and Tertil (1972) for *Apodemus agrarius*]. Values are means ± S.D. Each data point is a mean for several species (N is between two and five). The regression line (broken line) is given by metabolic reduction % $= -5.0 - 5.82 *$ group size ($F_{1,43} = 25.9$, $P < 0.001$). (B) The same data plotted as a function of ambient temperature for groups of two, three, four or five animals. There is no significant relationship between the reduction in energy expenditure and temperature ($F_{1,43} = 1.38$, $P = 0.246$). Each point represents a reduction in energy expenditure from one of the five studies. Mean values ± S.D are plotted in grey ($N = 7 - 12$).

temperatures, while other authors (Prychodko, 1958; Mount, 1960; McManus & Singer, 1975) report that energy benefits linked to huddling are negligible when ambient temperature increases and is within the thermoneutral zone. The data used in Fig. 4A were replotted in Fig. 4B as a function of ambient

temperature, and there was no significant relationship between reduction in energy expenditure when huddling and ambient temperature. From Table 3 it appears that adult birds or mammals huddling in groups of different sizes in response to temperatures lower than their thermoneutral

zone show a broadly similar reduction in metabolic rate to that of individuals exposed to temperatures within or close to their thermoneutral zone (mean ± S.D. 22 ± 13% and 22 ± 9%, respectively).

(3) Intensity of huddling

As described above, effectiveness and energy benefits of huddling depend primarily on the number of individuals involved in the group, and to a lesser extent on ambient temperature. Canals *et al.* (1998) predicted that for ambient temperatures close to the lower critical temperature, huddling effectiveness would be related only to the intensity of huddling (*i.e.* to the distance between individuals). Alberts (1978*a*) showed that huddling intensity is a function of ambient temperature in rats: the surface area of the huddle was positively correlated with ambient temperature. Mount (1960) reported that young domestic pigs (*Sus scrofa domesticus*) tend to increase inter-individual distances with increasing ambient temperature and Gilbert *et al.* (2008*b*) showed that the density of huddles of emperor penguins (*Aptenodytes forsteri*) varies with ambient temperature, being greater in poor environmental conditions (see Table 2). An increased intensity of huddling in response to lower ambient temperature is consistent with the fact that huddling is an active and group-related behaviour.

(4) Developmental stage and activity patterns

Developmental stage will influence huddling energy savings through variation in the capacity of individuals to change form and shape while they are grouped (Canals *et al.*, 1998). In house mice placed in groups of five at 20°C, juveniles show the maximum benefit from huddling (energy savings of 65%), followed by subadults (50%), and then adults (42%) (Canals *et al.*, 1998). By contrast, the metabolic rate of grouped tuco-tucos (*Ctenomys talarum*) younger than 15 days was the same as that of isolated individuals, whereas the metabolic rate of grouped tuco-tucos older than 15 days is reduced (Cutrera *et al.*, 2003). Gilbert *et al.* (2007*a*) showed that the thermoregulatory benefits of huddling were greater for rabbit pups (*Oryctolagus cuniculus*) younger than six days old when they are unable to thermoregulate independently.

Activity and body temperature rhythms can also modulate the energetic benefits of huddling. Tertil (1972) showed that the energetic benefits of huddling for striped field mice (*Apodemus agrarius*) varied according to their nycthemeral rhythm (*i.e.* alternation of diurnal and nocturnal phases) in activity and body temperature. A twofold metabolic reduction for grouped individuals at an ambient temperature of 20°C was recorded during the day (18%) compared with 9% during the active nighttime phase. These nocturnal rodents show reduced activity during the day which is associated with decreased body temperatures. However, when exposed to ambient temperatures of 5°C, metabolic reduction due to huddling was similar in the resting and active phases (23 and 20%, respectively).

According to Sokoloff & Blumberg (2001), heat production *via* the brown adipose tissue is involved in huddling in rat pups (*Rattus norvegicus*) where thermal cues affect the intensity of aggregation (Alberts, 2007). When non-shivering thermogenesis was inhibited, rats had a lower body temperature and did not compete efficiently to find preferential places within the huddle (Sokoloff & Blumberg, 2001). Sokoloff, Blumberg & Adams (2000) compared the huddling behaviour of rat pups aged 2–8 days, with functional brown adipose tissue, to eight day-old golden hamsters (*Mesocricetus auratus*), which are unable to produce heat *via* brown adipose tissue. Rat pups were more efficient in huddling, by adapting their huddle surface area to ambient temperature and decreasing to a higher extent their energy expenditure. A functional thermogenic capacity therefore seems to impact on the efficiency of huddling and consequently on its energetic benefits.

(5) Position within a huddle

Alberts (1978*b*) showed that huddling is an active group-regulated behaviour in which individuals constantly exchange position: rat pups (*Rattus norvegicus*) experiencing ambient temperatures lower than their thermoneutral zone tend to move to the centre of a group, in order to benefit from the warmth. By contrast, when ambient temperatures are within their thermoneutral zone, rat pups tend to occupy more peripheral places. Modelling suggests that more competitive individuals will occupy the better places, in the centre of the group, and therefore that all individuals will not necessarily receive identical benefits from huddling (Schank & Alberts, 1997). Recently, Bautista *et al.* (2008) investigated competition among 2–5 day-old rabbit pups (*Oryctolagus cuniculus*) for thermally favourable positions within the group. Calculating a huddling index as a measure of the degree of insulation the pups received, they found a positive correlation between mean huddling index and body temperature. However, there was no relationship between huddling index and birth mass, survival, milk intake, or milk to body mass conversion efficiency. It appears that newborn rabbits share thermally advantageous positions by continuously moving within the group. For birds, Noske (1985) showed that in clusters of varied sitellas (*Daphoenositta chrysoptera*), more dominant and older males acted as sentinels, protecting juveniles situated in the centre of the group. By contrast, in the case of bronze manikins (*Lonchura cucullatta*), dominant individuals obtained more advantageous positions in the centre of the group (Calf *et al.*, 2002). Hatchwell *et al.* (2009) reported that long-tailed tits (*Aegithalos caudatus*) individuals, occupying the peripheral positions in a linear roost formed during the night, lost significantly more (10%) mass, than individuals occupying inner positions. Gilbert *et al.* (2006) found no inter-individual differences in the time spent huddling per day by male emperor penguins (*Aptenodytes forsteri*): even though birds engage in several huddling and tight huddling bouts per day of variable durations, all breeders appear to benefit equally from regular and equal access to warmth.

VI. CONCLUSIONS

(1) Huddling is a complex social thermoregulation behaviour, defined as "an active and close aggregation of animals". It is used by a wide range of mammal and bird species.

(2) Huddling may be particularly important in energy conservation for species subjected to low seasonal or environmental ambient temperatures, in social species, and in species with poor insulation or with a high surface-to-volume ratio.

(3) Huddling reduces individual heat loss by minimizing cold-exposed surface area and by warming the local microclimate surrounding the group, and lowers energy production through lowering of body temperature, and possibly by psycho-physiological processes.

(4) Huddling conserves energy and allows individuals to increase their survival, lower their food intake, decrease their body mass loss, increase their growth rate, reduce their water use and maintain a more constant body temperature, through a significant reduction in their metabolic rate. Through huddling, mammals may reduce their energy expenditure by 8–53% and birds by 6–50%. The effectiveness of huddling varies according to group size, ambient temperature, intensity of huddling, age and species.

(5) Future research on huddling would benefit from further studies using the doubly labelled water technique, which can quantify the energetic benefits of free-ranging and undisturbed individuals in different conditions and over prolonged periods of time. Although it has been extensively shown that huddling is an energy conservation strategy, few studies have focused on the benefits that each individual may gain from this behaviour. Recently, Haig (2008) discussed the possible exploitation of shared warmth by some individuals in a multiple-paternity litter through genomic imprinting of brown fat tissue, which is the principal avenue of heat production in altricial mammals, enhancing huddling and aggregative behaviours. Huddling clearly is a complex cooperative behaviour which warrants further investigation.

VII. ACKNOWLEDGEMENTS

VIII. REFERENCES

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