Solitary versus group living lifestyles, social group composition and cooperation in otters

Thierry Lodé, Marie-Loup Lélias, Alban Lemasson, Catherine Blois-Heulin

Solitary *versus* group-living lifestyles, social group composition and cooperation in otters

Thierry LODÉ, *UMR CNRS 6552 ETHOS, University of Rennes 1, 35042 Rennes, France*

thierry.lode@univ-rennes1.fr (corresponding author)

Marie-Loup LÉLIAS, *LPPL, UPRES EA 4638, Université d'Angers, 49045 Angers Cedex 01. France*

Alban LEMASSON, *Institut Universitaire de France & UMR CNRS 6552 ETHOS, University of Rennes 1, Station biologique de Paimpont, 35380, Paimpont, France*

& Catherine BLOIS-HEULIN, *UMR CNRS 6552 ETHOS, University of Rennes 1, Station biologique de Paimpont, 35380, Paimpont, France.*

Small-clawed otters (*Aonyx cinereus)* (Photo Thierry Lodé).

ABSTRACT

Increased reproduction success, enhanced foraging and reduced predation risk are usually regarded as major factors favouring the evolution of social behaviour. Here we formulate a series of hypotheses relating sexual, ecological and behavioural factors to evaluate their explanatory value for 13 extant otter species, estimating the extent to which each factor contributes to the sociality of each species. We also compare individual behaviours within some of the species. Four otter species are obligatory social; four are obligatory solitary; five present both types of social organization. Social organizations of otter species are not related to their phylogenetic relationships. However, many otter species exhibit intra-species patterns of flexible social lifestyles. Both solitary and social otters adjust their social patterns in response chiefly to food availability, but also to habitat features and competition.

Group living is more common when intraspecific competition is reduced or trophic resources replenish rapidly. Under these circumstances, group members often forage individually. When otters forage individually, they often switch prey type when they compete with other conspecifics. Social structures of otters fall into seven types: 1) family groups; 2) extended family groups, often with an alpha dominant pair; 3) highly social groups with helpers; 4) collective hunting groups; 5) solitary life-style; 6) unstable mixed-sex groups; and 7) single-sex bachelor groups. When an individual of a species with variable sociality adopts one type of sociality, this may be only temporary. Variations in social life are actually based on a series of events that induce individuals to make decisions taking ecological factors into account.

Although ontogenetic factors can influence delayed dispersal of otters, social factors rather than ecological factors could play an important role in the formation of groups, and cohesiveness and kinship appear to be secondary effects of reduced

dispersal more than primary causes for living in a group. Appropriate adjustment of group behaviour reduces the cost of sociality because individuals avoid social interactions when benefits are low but gather together when group-living provides real advantages. Although any one model is unlikely to explicate all facets of sociality, evolution towards a social group results mainly from interactions within a family.

Keywords cooperation, delayed dispersal, kin selection, parental care, reproductive skew

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INTRODUCTION

Despite decades of research focusing on social and cooperative animals, many questions concerning the evolution of group-living systems are still unresolved (Axelrod 1984, Pennisi 2005). How are group-living benefits to be understood in the context of Darwinian competition for survival? Simply, group living is theorized to evolve when fitness benefits obtained by one individual within a group outweigh the costs of sharing key resources with conspecifics (Koenig et al. 1992; Cockburn 1998; Hatchwell and Komdeur 2000; Macdonald and Carr 1989; Bacon et al. 1991a, b; Johnson et al. 2000; Johnson et al. 2002b) and/or when there are strong ecological constraints on independent reproduction (Von Schantz 1984b; Lindström 1986; Hatchwell and Komdeur 2000). During the last few decades, this question has been debated within a diversity of theoretical frameworks (see West et al. 2007), but attention has focused especially on some highly social species.

Numerous advantages have been listed to explain why animals live in social groups. Increased reproduction success, enhanced foraging success and reduced predation risk are usually regarded as the major factors affecting the evolution of social behaviour (Hamilton 1964, Alexander 1974, Clutton-Brock 2002, Clutton-Brock et al. 2001). Nonetheless, these potential benefits can be broadly offset by costs linked to promiscuity resulting from living in groups, and natural selection should favour non-cooperative selfish individuals (Creel 1997, West et al. 2002, Couzin 2006). Social animals face higher risks of disease and parasitism (Drewe 2009). Large groups are more susceptible to be detected by predators and put greater pressure on trophic resources leading to unequal delivery of food and increasing aggression among animals (Clutton-Brock et al. 2001, Krause and Ruxton 2002, Brewer 2008). Living in a social group could also lead to inbreeding or aggressive competition to find a mate and to raise young and infanticide between competing mothers. Finally, from an evolutionary

87 point of view, why non-breeding individuals tolerate group-living and even help breeding
88 conspecifics remains one of the most relevant questions (see Kokko and Johnstone
89 1999).

90 Although authors usually distinguish three aspects of social systems: social
91 structure, care and mating systems, the need has emerged recently to differentiate
92 between social structure, structural aspects of interactions within a society, and social
93 organization, size and composition of the social unit (Prox and Farine, 2020). In fact,
94 animal species exhibit a large diversity of social systems, social organisation and group-
95 living structure can vary within a zoological taxon (Reiczigel et al. 2008). For example,
96 the social organizations of numerous species of otters vary considerably from solitary
97 life (*Lutra lutra*, Kruuk and Moorhouse 1991*, Lontra longicaudis*, Rheingantz et al.
98 2017), to monogamous pairs (*Lontra felina*, Ostfeld et al. 1989), or extended family
99 groups (*Pteronura brasiliensis,* Duplaix 1980, Ribas et al. 2016, Schmelz et al. 2017)
100 and sometimes groups of males (*Aonyx capensis*, Arden-Clarke 1986; *Lontra*
101 *canadensis,* Blundell et al. 2002a) (Table 1). Nevertheless, otters of the monophyletic
102 subfamily Lutrinae (Bininda-Edmonds et al. 1999, Koepfli and Wayne 1998, Koepfli et
103 al. 2008) reveal morphological similarities and present comparable amphibious habits
104 and ecological requirements (Mason and Macdonald 1986, Kruuk 2006, Raha and
105 Hussain 2016). Otters exhibit an elaborate range of societies and the combination of
106 variable mating systems, social organizations and ecological and social characteristics
107 provides a rare opportunity to analyse the importance of factors which could influence
108 otters' social habits. The way social groups are categorized could help unravel factors
109 arising from the environment or life histories (Prox and Farine 2020).

110 Here we formulated a series of hypotheses relating sexual, ecological and
111 behavioural factors. For each hypothesis, we explain first its theoretical foundation, then

we evaluate its explanatory value for 13 otter species, indicating the extent to which each factor contributes to the sociality of each species.

Finally, by inspecting for parsimony among explanatory factors, we determine whether otter sociality is the consequence of any single factor or a combination of factors, across species. By focusing on the Lutrinae we hope to illustrate how theoretical models could be applied to animals in order to discern future directions of the social ecology paradigm.

INTERSPECIFIC VARIATION OF SOCIALITY

Questioning advantages of kin group-living

Sociality is theorized to evolve when the benefits of group living exceed the costs (Axelrod 1984; Krause and Ruxton, 2002), but the role played by kinship in establishing social bonds needs to be evaluated.

Analyses of costs and benefits of sociality have often been made using Hamilton's rule on "Kin Selection" (Hamilton 1964). Kin selection favours the fitness of relatives at the expense of one's own survival and reproduction. Usually, "altruistic" behaviours are incorrectly called "cooperative" although they are not reciprocal and they reduce individual reproduction success (Wilson 1990). While cooperative interactions are supposed to be mutually beneficial, altruistic behaviours involve non-reproductive subordinates helping dominant individuals during the breeding period. The introduction of the "kin selection" concept stimulated fruitful research on group-living animals, although relatedness among haplodiploid hymenoptera is higher than among other animals (Foster et al. 2006). For instance, genetic relatedness seems to predict the organization of social groups of dwarf mongooses *Helogale parvula* (Creel and Waser

1994), kinkajous *Poto flavus* (Kays et al. 2000) and wild African elephants *Loxodonta africana* (Archie et al. 2006). Unsuccessful long-tailed tit (*Aegithalos caudatus*) breeders can act as helpers in the nests of close kin when the chance of successful independent reproduction is low (Hatchwell & Sharp 2006). Male lion coalitions tend to consist of closely related individuals (Spong et al. 2002) and group-living females exhibit a high relatedness favouring their counter-action against infanticide (Mosser and Packer 2009).

Kin-mediated philopatry and cooperation benefits have been reported for numerous species. Assuming that the genes that promote altruistic behaviour favour increased feeding efficiency for instance suggests that this drives to produce a strong correlation between donor and recipient (Wilson 1990, Okasha 2002). Furthermore, limited or delayed dispersal increase the opportunities to interact with kin, and this could promote the evolution of cooperative breeding (Hamilton 1964). Nonetheless exploiting a resource by kin may also dramatically increase competition thus reducing all the benefits of cooperation.

Cooperative and altruistic kin-related behaviours could be maintained by other factors even in closely related groups and individuals presumed to be non-helpers could be cooperative (Komdeur 2006). Thus, the risk of predation considerably affects the pattern and time-budget of feeding. Sentinel behaviour in cooperative groups has been regarded as a form of altruistic anti-predator vigilance providing protection for the entire group (Hailman 1994). The alarm calls of Belding's ground squirrels (*Spermophilus beldingi*) indicate that sentinels alarm relatives and should be the result of kin selection (Sherman 1977). While sentinels take the risk of vocalizing, other individuals can increase time devoted to feeding (Manser 1999, 2001). Townsend et al. (2011) reported that meerkats are less vigilant when exposed to specific calls indicating that an individual has briefly scanned the surrounding environment for predators. Although the

function of sentinels assures a cooperative vigilance (Wright et al., 2001b) it could emerge from individually selfish antipredatory behaviour (Blumstein 1999).

Whereas kin selection could underlie the evolution of some cooperatively breeding societies, this body of theory can hardly explain why some closely related species are not social while other species, exposed to similar ecological conditions, exhibit a complex social life. Thus, the absence of relatedness over the whole genome results in a strong selection for suppression of cooperative behaviour because the supposed altruistic gene would be in conflict with genes elsewhere in the genome (Grafen 2006, Helantera and Bargum 2007, West et al. 2007). Furthermore, when dispersal is reduced competition among kin can affect reproduction and can reduce, and even totally counteract, all kin-selected benefits for relatives (Griffin and West 2002, West et al. 2002, Gardner and West 2006). Consequently, it seems that sociological foundations prevail over purely kin factors.

It is often difficult to disentangle kin from non-kin mechanisms that promote group-living (Keller 1997). The North American river otter lives in large groups in marine environments (Rock et al. 1994; Larivière and Walton 1998) in habitats including inshore complexity and less reduction of foraging opportunities in winter than on inland lakes and rivers due to less freeze-up. Analysing the role of relatedness in these social habits, Blundell et al. (2004) rejected the hypothesis that social groups of otters were kin based. Group-living otters inhabiting coastal habitats included a group of individuals that were not related, as well as some that were closely related and both sexes exhibited a low probability of natal dispersal (Blundell et al. 2002b). Giant otters live in highly cooperative groups but Ribas et al. (2016) reasoned that direct benefits, such as alloparental care, and defence of high-quality home-ranges may have driven the development of sociability in this species. Small-clawed otter *(Aonyx (Amblonyx) cinereus*) groups are known to include unrelated juvenile adults (Foster-Turley 1992,

190 Furuya 1976). Kin recognition mechanisms of mustelids do not differ clearly from
191 specific recognition of familiar but unrelated conspecifics (Lodé 2008, Hansen et al.
192 2009). Oriental small-clawed female otters discriminated between familiar and
193 unfamiliar adult males based on their sound and odour (Lemasson et al. 2013). Indeed,
194 relatedness among group members of numerous carnivores can be high, especially
195 when dispersal is restricted (Creel and Waser 1994, Girman et al. 1997, Gompper et al.
196 1997, Clutton-Brock 2002). Kin-structured populations can occur in solitary species
197 when their dispersal is restricted, as in cooperative species (Shorey et al. 2000, Lodé
198 2001, Foerster et al. 2006, Wagner et al. 2007), thus indicating that kin selection is not a
199 necessary condition for cooperation to emerge. Indeed, collective hunting by otters does
200 not require association with kin (Blundell et al. 2002b, Schmelz et al. 2017), resulting in
201 no selection pressure for kin-based groups. Therefore, although kinship undoubtedly
202 promotes social tolerance, it could be argued that the kinship observed in some highly
203 social animals could be a secondary effect of reduced dispersal and colonial living
204 rather than a primary cause for group living when their natal territories can support food
205 requirements.
206
207 **Sociality and phylogeny**
208 Based on the phylogenetic relatedness within the taxon Lutrinae, we would expect to
209 identify fairly similar social phenotypes. Lutrine otters form a monophyletic family which
210 diverged from other mustelids about 20-25 million years ago (Koepfli and Wayne 1998),
211 but variations of sociality among species appears to be unrelated to their taxonomic
212 positions (Kruuk 2006). Thus, the social organizations of otters seem not to be
213 associated with phylogenetic relationships, as measured through super-tree
214 constructions (Bininda-Edmonds et al. 1999, Koepfli et al. 2008) (Fig. 1). The social
215 structures, mating systems and behaviour of many otter species are not well known but

both the largest (the giant otter) and the smallest species (the small-clawed otter) are reported to develop strong social interactions (Kruuk 2006). Two species of the genus *Lontra* remain strictly solitary, while two other species apparently can adopt a more social behaviour depending on the circumstances. Indeed, otters seem to exhibit very variable social patterns: social, flexible and solitary.

While marine otters (*Lontra feline)* or spotted-necked otters (*Lutra (Hydrictis*) *maculicollis)* often exhibit solitary habits (Lejeune 1989, Angelici 2005), these species can live in small family groups in numerous occasions (Ostfeld et al. 1989, Kruuk & Goudswaard 1990**,** Medina-Vogel et al. 2006). In contrast, both southern river otters *(Lontra provocax)* (Larivière 1999, Sepúlveda et al. 2007), hairy-nosed otters (*Lutra sumatrana)* (Sivasothi and Nor 1994, Nguyen et al. 2001; Nguyen 2005, Kanchanasakha 2007) and Neotropical river otters (*Lontra longicaudis)* (Helder and DeAndrade 1997, Kasper et al. 2008, Rheingantz et al. 2011, Rheingantz et al. 2017*)* are mainly solitary, whereas North American river otters (*Lontra canadensis*) (Melquist & Hornocker 1983, Rock et al. 1994, Larivière & Walton 1998, Blundell et al. 2004) and European otters (*Lutra lutra)* have both solitary and social habits (Mason & Macdonald 1986, Kruuk & Morhouse 1991). Smooth-coated otters (*Lutrogale persipicillata)* can live in small family groups (Foster-Turley 1992, Sivasothi & Nor 1994, Hussain 1996, Khan et al. 2010). Congo clawless otters (*Aonyx congicus)* privilege solitary habits (Larivière 2001, Jacques et al. 2009), whereas African clawless otters (*Aonyx capensis)* (Arden-Clarke 1986, Ostfeld et al. 1989, Creel & Mcdonald 1995) and small-clawed otters (*Aonyx (Amblonyx) cinereus),* often have social habits (Furuya 1976, Foster-Turley 1992, Hussain et al. 2011). Finally, giant otters (*Pteronura brasiliensis)* (Duplaix 1980, Carter and Rosas 1997, Leuchtenberger and Mourão 2008) and sea otters (*Enhydra lutris)* (Garshelis et al. 1984, McShane et al. 1995) are highly social.

241 Socially, otter species therefore have less in common with other species of the
242 same genus than they have with other less closely related phylogenetically otter species
243 (Kruuk 2006). This suggests that otters' social life style does not depend on genetic
244 relatedness.
245
246 **Group-living and dispersal**
247 We questioned whether social life style could depend on factors delaying dispersal of
248 juveniles. Limited dispersal can indeed engender a relatively high level of relatedness
249 among populations. Kin-patterns could be a by-product of dispersal patterns as similar
250 patterns are observed in solitary species. Koenig et al.'s (1992) "Delayed-Dispersal
251 Threshold Model" proposed that delayed dispersal could be one of the most important
252 processes of social life because it generates kin-structured groups without requiring any
253 kin discrimination mechanism. This hypothesis thus clearly predicts that breeding
254 dispersal will be lower in cooperative species than in non-cooperative species.
255 Could dispersal of juvenile otters be limited by the reduction of available
256 territories? Habitat saturation is regarded as the main constraint inducing breeding
257 individuals to delay breeding but fails to explain the evolution of delayed dispersal
258 (Koenig et al. 1992). The "Habitat Saturation Hypothesis" has been tested through
259 manipulation of populations of birds and fishes but results were variable (Komdeur
260 1992, Bergmüller et al. 2005, Stiver et al. 2006). Authors have demonstrated that the
261 reproduction success of cooperative carrion crows *Corvus corone* (Canestrari et al.
262 2008) increases with group size but investigating the ecology of delayed dispersal
263 Baglione et al. (2005) observed that philopatry in the carrion crow occurred mainly in the
264 less competitive and less variable environments and that cooperative breeding and
265 delayed dispersal appeared to be independent of the availability of suitable breeding
266 habitats for subordinates (Baglione et al. 2005). Dispersal distances varied strongly

267 within a species revealing extremely flexible dispersal strategies (Le Galliard et al.
268 2012) and dispersal could be more environmental condition-dependent than expected
269 (Bowler and Benton 2005). Thus, resource availability may drive group size.

270 Parental care has been argued to be a precondition for limited dispersal and
271 therefore, should promote a mechanism similar to, or undistinguishable from, kin-group
272 selection. However European badgers' parental care may be very limited after weaning,
273 but their dispersal is limited as long as their habitat does not appear to be saturated.
274 Examining the genetic structure and the mating system of Coquerel's dwarf lemur
275 (*Mirza coquereli*), Kappeler et al. (2002) discussed "hidden" effects of kinship in the
276 dispersal systems of apparently 'solitary' animals. They found that apparent 'solitary'
277 individuals are structured in matrilines. As a result, paternity was widely spread among
278 males and mixed paternities existed. The philopatry of solitary carnivore raccoon
279 (*Procyon lotor*) females also influences the genetic structure of the entire population
280 (Ratnayeke et al. 2002). Similarly, male-biased dispersal and female philopatry basically
281 favour the social organization of corvids (Williams and Rabenold 2005). Species exhibit
282 wide dissimilarities in dispersal strategies with no clear tendencies between solitary or
283 cooperative species (Clobert et al. 2001). Dispersal distances of mammals are
284 proportional to the size of their home-range, considering body size independently
285 (Bowman et al. 2002). Emigration governs group dynamics and, indeed, cooperation
286 appears more extensive among individuals of the sex that are less likely to disperse,
287 mostly females (Wrangham and Rubenstein 1986). Furthermore, although limited
288 dispersal can favour cooperation, it can also generate competitive interactions,
289 especially between mates. Limited and delayed dispersal seems therefore to be a
290 process similar to kin selection because constraints on dispersal have entailed the
291 development of kin-structured populations.

292 Mustelids' dispersal is often male-biased (Lodé 2001, Blundell et al. 2002b,
293 Mcdonald et al. 2008) and this is generally regarded as promoting avoidance of
294 inbreeding (Pusey 1987, Perrin & Mazalov 2000). Polygyny should favour philopatry of
295 the limiting sex and dispersal of the other (Greenwood 1980), increasing the operational
296 sex-ratio bias (ratio of breeding adults), so that males do not have the opportunity to find
297 mates. Living in aquatic ecosystems and often in linear water courses could constitute a
298 severe constraint to dispersal, and patterns of dispersal of breeding subaquatic
299 mustelids proceed according to the stepping-stone model (Gadgil 1971, Sjöåsen 1997)
300 in which sub-population exchanges are favoured in contiguous zones (Lodé 2002,
301 Bifolchi and Lodé 2005). Thus, European otters exhibit only limited dispersal
302 movements (Kalz et al. 2006). A relatively high proportion of sea otters could however
303 be long-distance dispersers (Krkosek et al. 2007).

304 The formation of male groups appears to be linked to reduced dispersal and to the
305 philopatry of females in polygynous species in which habitat saturation might occur.
306 Single-sex groups are observed in some species, leading to male bachelor social
307 congregations (Pope 1990, Ruckstuhl and Neuhaus 2000). By forming coalitions,
308 species regarded as solitary, such as cheetahs (*Acinonyx jubatus*) and slender
309 mongooses (*Herpestes sanguineus*) are expected to forage more successfully and to
310 have better access to females (Caro and Collins 1987, Waser et al. 1994). Genetic
311 similarity among siblings facilitates male coalitions and cooperation (Packer et al. 1991,
312 Waser et al. 1994, Kays et al. 2000, Möller et al. 2001, Spong et al. 2002). When
313 members of these alliances are related, they can benefit indirectly when the alliance
314 enhances their future reproduction success (Packer et al. 1991, Kays et al. 2000, Mitani
315 et al. 2000). Sea otters (Garshelis et al. 1984, Pearson and Davies 2005), African
316 clawless otters (Arden-Clarke 1986) and North American river otters (Blundell et al.
317 2002a) can form male bachelor congregations but they do not always hunt together and

318 do not form any coalition for mates. This suggests that mechanisms other than kinship
319 are involved in the formation of groups of males (Griffin and West 2002).
320
321 **SOCIOECOLOGICAL AND LIFE-HISTORY RELATED HYPOTHESES**
322
323 **Ecological constraints**
324 Could the strong constraints of aquatic habitats also weigh on the emergence of the
325 otters' social life? Although otters live in aquatic habitats and have relatively similar
326 ecological requirements, the different species present a great diversity of social
327 structures, including solitary habits and group-living. Similarly, the social structures and
328 mating systems of dolphins vary although they live in marine habitats and while the killer
329 whales (*Orcinus orca*) travel in extremely stable social groups, most dolphin species
330 appear to have a more fluid social organization (Tyack 1986, Baird et al. 1992, Möller et
331 al. 2001). By contrast, and although mongooses are known to show greatly complex
332 social organizations associating adult breeders and helpers, water mongooses (*Atilax*
333 *paludinosus*) live a strict solitary life despite the use of aquatic habitats (Ray 1997).
334 Thus, we reason that freshwater ecosystems do not impair the social life style of
335 animals.
336 However, might ecological requirements and habitats in which a population
337 resides influence whether or not a species lives a social life? Predator avoidance and
338 the monopolization of food resources are often the two ecological hypotheses preferred
339 to explain the formation of social groups (Alexander 1974, Wrangham and Rubenstein
340 1986, Bergmüller et al. 2005, Ylönen and Brown 2007). Obviously, living in social
341 groups facilitates cooperation for foraging and defence (Smith et al. 2012). Proposing
342 the “ecological constraints hypothesis” Smith et al. (2008) showed that cooperation
343 could increase individual benefits for trophic resources and defence. The scarcity of

344 breeding sites has been evoked as a key factor determining cooperative breeding in
345 birds (Koenig et al. 1992, Cockburn 1998). Analysing natal philopatry and cooperative
346 breeding of Siberian jays (*Perisoreus infaustus*) Kokko and Ekman (2002) realized that
347 “ecological constraint" is a term too wide to yield useful predictive power.

348 Nevertheless, low availability of resources could affect cooperative strategies
349 significantly. In his detailed review of the literature available at that time, Powell (1979)
350 proposed that the social organizations of mustelids were fundamentally based on intra-
351 sexual territoriality, with male home-ranges overlapping those of females. Basically,
352 dependent on food resources, this spatial organization seems to form a socio-ecological
353 pattern that is very common in carnivores (Johnson et al. 2000**).** Dispersion of resource
354 patterns could drive socio-spatial organization, allowing some species to congregate
355 with variable social organization (Macdonald & Newman 2018). All otter social systems
356 are considered as variations on a theme of female territories overlapped by larger male
357 territories (Kruuk 2006).

358 The “Resource Dispersion Hypothesis (RDH)” (Macdonald 1983, Carr and
359 Macdonald 1986, Johnson et al. 2002, Macdonald and Sillero-Zubri 2004) argues that
360 when resources are heterogeneously distributed, group living may be less costly, even
361 without cooperative behaviour. This resource-based hypothesis proposes that patchy
362 resources favour the overlap of conspecific home-ranges, leading to the promotion of
363 social life. The main predictions are that *i)* home range size would be independent of
364 group size, *ii*) home-range size would increase with dispersal of prey, *iii)* but group size
365 would be affected by resource heterogeneity and *iv)* by resource patch richness. The
366 social organisation of the British populations of European badgers (*Meles meles*) was
367 found to be coherent with the HDR hypothesis (Carr and Macdonald 1986). However,
368 Mbizah et al. (2019) investigating lion groups could not confirm some of the HDR
369 predictions since the evaluations of resource heterogeneity and resource patch richness

370 did not show any significant effects on the size of lion groups. The sizes of European
371 badgers' territories in Spain were shown to be related to their richness rather than to
372 patch dispersion (Revilla and Palomares 2002). During the non-breeding season males
373 of numerous mustelids can maintain their territories for the defence of offspring
374 (Schröpfer et al. 1997), but by marking home-ranges actively males can also defend
375 future mating opportunities. Therefore, the resource dispersion model can describe
376 some environmental constraints restricting or favouring group-living rather than those
377 driving social life (Revilla 2003, Verdolin 2009).

378 Nevertheless, following RDH, could groups be formed because mixed resources
379 dispersed in space and time are indefensible individually? Although most reports are
380 based on local data from one particular habitat / density region, the flexibility of social
381 systems suggests however a slightly more complex situation. Groenendijk et al. 2015
382 conclude that giant otter societies are probably shaped by the spatial dispersion of lakes
383 and food abundance and dispersion within these rich patches, while North American
384 river otters have clearly broken some expectations. Indeed, many individuals exhibit
385 roaming excursions and mustelids often show a high level of intolerance even between
386 males and females and territoriality can sometimes be absent (Erlinge and Sandell
387 1986, Lodé, 1996a). Otters are often found to exploit aquatic organisms patchily in river
388 courses, seashores and lakes but both solitary and group-living otters exhibit a similar
389 pattern of resource utilization (Brzezinski et al. 1993, Rowe-Rowe and Somers 1998,
390 Rosas et al. 1999, Somers & Nel 2003, Medina-Vogel et al. 2004, Parker et al. 2005,
391 Medina-Vogel and Gonzales-Lagos 2008; Córdova et al. 2009, Cabral 2010,
392 Rheingantz et al. 2011). In addition, North American river otters' home-range sizes
393 decrease with sociality, thus challenging the first prediction of the RDH (Blundell et al.
394 2002a). Nonetheless, in order to validate these views, we would need more data
395 concerning different populations of the same species.

Reciprocal altruism

Cooperative breeding means that the quality of interactions among conspecifics is privileged, often promoting the emergence of 'altruistic' behaviours. What behavioural rules make it likely that social groups will be formed? Nepotism can lessen conflicts between selfish interests but authors now commonly admit that helpers are less closely related to breeders than previously suspected (Clutton-Brock 2002), so how could unrelated helpers benefit from progeny care?

Trivers' (1971) Reciprocal Altruism Hypothesis emphasized that group-living and cooperation could result from reciprocal interactions providing mutual benefits. 'Reciprocal altruism' allows that altruistic acts exist between unrelated individuals as well as between relatives. This requires that individuals interact often and are able to recognize individuals with whom they have interacted. West et al. (2007) suggested that the use of the term 'mutual benefit' would be more correct. In a reciprocal cooperation, individual cost of cooperation is offset by long-term benefits of being helped, and helpers must be able to identify cheaters (Sachs 2004, West et al. 2007). For instance, blood sharing regurgitation by vampire bats (*Desmodus rotuntus*) is interpreted as 'reciprocal altruistic' food sharing (Denaut and McFarlane 1995). The formation of male baboon (*Papio anubis*) coalitions has been understood as an example of 'reciprocal altruism' (Packer 1977). Similarly, green woodhoopoes (*Phoeniculus purpureus*) exhibit behaviours that appear to meet all the criteria of reciprocity between unrelated helpers (Ligon and Ligon, 1983). At least three otter species present cooperative foraging and food sharing behaviours that seem to respond to a sort of reciprocal altruism.

Numerous examples of *pseudo-reciprocity* promoting self-serving behaviour have been mentioned in the literature (West et al. 2002). Unlike sentinel behaviour, helpers are however characterized by the asymmetry of the interaction because 'altruistic'

422 individuals contribute care to offspring at the expense of their own progeny. Reciprocal
423 cooperation could be encouraged by a high rate of mortality that leads to the evolution
424 of these mutually beneficial interactions. Such events should act as enforcement
425 because they influence both the cost and benefit of cooperating (West et al. 2007).
426 Numerous species of group-living otters present sentinel behaviour, and at least,
427 three otter species include helpers, i.e. cooperative foraging, food sharing and collective
428 defence against predators by unrelated adults, yearlings or juveniles. Cooperative
429 helpers are observed in Giant otters (Duplaix 1980, Davenport 2010, Groenendjik et al.
430 2014, Schmelz et al. 2017) and in American river otters (Rock et al. 1994, Larivière &
431 Walton 1998, Blundell et al. 2002a). The average relatedness within groups of Giant
432 otters was high, but the degree of relatedness could vary within groups that included
433 unrelated individuals, contradicting the current social hypothesis of a parent brood
434 model (Ribas et al. 2016). Although the social structure of small-clawed otters has not
435 yet been studied in detail in the field this species is considered the most social
436 (Johnson et al. 2000) and many authors report that a group shares a nest and behaves
437 as a social unit, that individuals practice allogrooming and “interactive games”, and that
438 siblings can help raise offspring, the alpha pair being dominant (Furuya 1976, Pellis
439 1984, Foster-Turley 1992, Sivasothi and Nor 1994, Sivasothi 1996, Larivière 2003,
440 Kruuk 2006; Prakash 2010, Hussain et al. 2011, Perdue et al. 2013).
441 To reproduce successfully, animals require territories with good trophic
442 availability and have to find sexual partners. The pay-to-stay hypothesis argues that
443 help at nest constitutes a kind of “rent” paid to a dominant for being allowed to live in the
444 dominant’s home-range. So, rather than attempt to breed with difficulty after a
445 dangerous dispersal trip, it may be reasonable to remain for one more year within the
446 family, delaying breeding opportunity, to acquire better survival probability and parental
447 experience (Komdeur 1996, Kokko and Johnstone 1999). This acquisition of experience

448 could be one of the indirect gains of cooperative breeding (Clutton-Brock 2002) and is
449 obtained by waiting for better dispersal opportunities, especially in unpredictable
450 environments, so that cooperative breeding could appear to be making 'the best of a
451 bad job' (Rubenstein and Lovette 2007). Nevertheless, such indirect benefits do not
452 seem to play a crucial role for western bluebird (*Sialia mexicana*) helpers' fitness
453 (Dickinson 2004). Mechanisms rewarding helpers are assumed to be more common
454 and more effective for maintaining cooperative breeding than punishment (Snowdon
455 and Cronin 2007). Conversely, direct enforcement mechanisms, such as harassment,
456 may not result in complete repression of within-group competition.
457 Competition for resources among individuals can then defeat cooperative
458 behaviour (Gardner and West 2004) and furthermore, by remaining with their family
459 individuals become subordinates in the kin group and may lose their chance to breed.
460
461
462 **INTRASPECIFIC VARIATION IN SOCIALITY**
463
464 **Variations in reproductive opportunity**
465 As social groups incorporate adults, how could competition for mates influence social
466 life? The avoidance of inbreeding amongst closely related within-group kin could drive
467 suppression of reproduction and/or drive extra-group kleptogamy. Reproduction ability
468 variation among group members is called 'reproductive skew'. Indeed, group-living often
469 inhibits subordinates' breeding (Wasser and Barash 1983). Basically, non-breeding
470 individuals endure an intrinsic conflict concerning reproduction as they receive complex
471 social and physiological messages implying social dominance, harassment and
472 glucocorticoid stress (Creel 2001, Mech and Boitani 2003, Goymann and Wingfield
473 2004, Bennett 2009, Rubinstein and Sheng-Feng 2009). Thus, dominant adults of

474 different mongoose species manipulate subordinates to suppress all their reproduction
475 opportunities (Creel et al. 1992, Cant 2000, Clutton-Brock et al. 2004). In fact, behavioural
476 inhibition of subordinates' reproduction abilities could be one of the keys to carnivores'
477 social life (Creel and McDonald 1995). While the 'Optimal Skew Model' of reproductive
478 suppression assumes that dominant pairs monopolize reproduction preventing
479 subordinates from breeding (Vehrencamp 1983, Reeve and Keller 1995), Cant (2000)
480 argued that control by the alpha pairs is chiefly social and often remains incomplete,
481 sometimes allowing subordinates to reproduce more or less successfully. However,
482 different models of reproductive skew seem to be declinations of a general theory,
483 rather than alternative paradigms (Johnstone 2000).

484 Reproductive skew and dominance are not well known for most of the otter
485 species, but the social structure of many otter species could suggest such a
486 characteristic. Small-clawed otters and North American river otters form monogamous
487 pairs but several individuals, up to thirteen, including young and helpers can live
488 together (Furuya 1976, Pellis 1984, Foster-Turley 1992, Rock et al. 1994, Sivasothi
489 1996, Blundell et al. 2002a, Prakash 2010, Hussain et al. 2011, Perdue et al. 2013). A
490 group includes a dominant pair of male and female adults and the hierarchical
491 organization of the group around this alpha pair suggests a possible influence of low
492 reproduction conflict and parental manipulation, inhibiting subordinates' mating.
493 Similarly, only the original giant otter parents, the alpha pair, generally breed during
494 their lifetime and juveniles behave as helpers (Duplaix 1980, Davenport 2010;
495 Groenendjik et al. 2014). Nevertheless, subordinates, and especially females, can
496 sometimes breed in some populations of giant and small-clawed otters.

497 Competition for access to sexual partners is a fundamental component of sexual
498 selection, and dominance interactions result in inhibition or suppression reproduction of
499 group-living subordinates without requiring individuals to be closely related.

500 Nevertheless, close relatedness could increase tolerance to manipulation, especially
501 since the individuals forming a group generally originate from the same family. Thus,
502 evolution towards social groups could result from interactions within family groups
503 implying dominance and harassment that suppress subordinates' reproduction
504 opportunities. The alpha pair of meerkats (*Suricata suricatta*) increases survival rates of
505 their progeny by harassing subordinates (Griffin et al. 2003, Young et al. 2006).
506 Although reproduction opportunities amongst individuals of different ranks often show
507 that dominant individuals accrue greater reproduction benefits than subordinates,
508 banded mongooses (*Mungos mungo*) have been found to exhibit low reproductive
509 skew, suggesting that the societies of some social species such as banded mongeese
510 could be relatively egalitarian (Luca and Ginsberg 2001). Similarly, dwarf mongoose
511 subordinates can reproduce sometimes (Keane et al.1994).
512
513 **Variations in social patterns**
514 Most studies dealing with ecological constraints concern different morphologically
515 dissimilar species and different ecological resources. By contrast, otters show similar
516 amphibious habits and exhibit comparable ecological requirements although specific
517 social structures vary greatly. Many otter species are known to fluctuate intra-
518 specifically from solitary lifestyle (often called 'solitary' species) to group-living
519 organizations whereas other species exhibit stable social traits (Fig. 2). 'Solitary'
520 however does not mean asocial. The term 'solitary' applied to a species is misleading
521 because it ignores both indirect social interactions and social phases, *i.e.* between
522 sexual partners or mother-cubs relationships for instance and I proposed that it could be
523 replaced by the term 'individualistic' (Lodé et al. 2003), not in its pejorative sense, but
524 meaning independent lifestyle. European otter populations can exhibit solitary ways of
525 life as well as social habits in some parts of their range (Kruuk 2006, Quaglietta et al.

526 2014). Indirect social interactions through olfactory marks give extensive information
527 about conspecifics and the social organization of solitary species is mainly based on
528 odours. Solitary species such as polecats *Mustela putorius* (Lodé 2008) or social small-
529 clawed otters (Lemasson et al. 2013) are capable of olfactory recognition.

530 Variations of social patterns illustrate that the term 'social life' encompasses
531 numerous situations which are sometimes called 'solitary', 'subsocial', 'familial',
532 'eusocial' or 'highly' social. Quantitative measures of social level were proposed to
533 estimate, along a sociality scale from solitary to eusocial, the 'tendencies of individuals
534 to live in groups' as a result of philopatry, to exhibit reproduction altruism and
535 conspecific tolerance (Nonacs 2000, Reiczigel et al. 2008, Bang et al. 2009, Avilés and
536 Harwood 2012). In fact, the current consensus concerning group-living animals
537 hypothesizes a selection progressively leading towards more elaborate forms of
538 sociality, presupposing a 'solitary' ancestral state (Creel & McDonald 1995, Véron et al.
539 2004, Dalerum 2007, Schultz et al. 2011, Smith et al. 2012). Nonetheless, we can
540 imagine a more flexible ancestral state so that some species' solitary habits may stem
541 from ancestors exhibiting a flexible social organization (Dalerum 2007). Thus, although
542 four American otter species are phylogenetically closely related, they exhibit very
543 divergent social traits, neotropical river otters and southern river otters live solitary lives
544 although they have only recently diverged from North American otters and marine otters
545 that can live in small family and social groups. Species showing solitary habits are
546 equally distributed across the three continents (two species in Africa, two species in
547 America and two species in Eurasia), conversely four of the seven group-living otter
548 species are found in America, only one in Africa and two in Eurasia, showing weak
549 differences among continents.

550 For sociality to evolve, the benefits of living in a group must outweigh the costs.
551 (Krause and Ruxton 2002). In fact, Silk (2007) argued that the difficulty to link the

552 effects of behavioural interactions to fitness explains why sociality varies across species
553 and habitats. Following Emlen and Wrege (1994) and Emlen et al. (1995), social
554 behaviour can however be consider as a series of decisions made by an individual
555 during its lifetime. As a component of social strategy, each behavioural option can
556 influence an individual's fitness and staying within the familial group could therefore
557 represent the 'best of a bad job', promoting future cooperation. Subordinates could
558 obtain some benefits by staying as helpers. Thus, delayed dispersal would be the best
559 decision when numerous competitors or predators are present and prolong the benefits
560 of parental care (Ekman et al. 2001, Kokko and Ekman 2002). Females may inherit the
561 home-range of their mother whereas males could be obliged to delay their dispersal
562 until they have the opportunity to find an available territory and a mate, because many
563 females stay in their parental territories. In return, groups can help prevent receptive
564 females from invading 'floater' individuals. Such anti-harassment behaviour is observed
565 in baboons (Lemasson et al. 2008). Finally, female sociality could allow the best access
566 to patchy resources when faced with competing males. Thus, the social system of
567 female white-nosed coatis (*Nasua narica*) favours their foraging success whereas larger
568 males are able to compete for food without living in groups (Gompper 1996). Group-
569 living patterns of communally rearing rodents (*Octodon degus*) vary according to food
570 availability and predation (Ebensperger et al. 2012).

571 While striped mice (*Rhabdomys pumilio*) show solitary habits in grassland but in the
572 arid succulent karoo they live in social groups comprising multiple adults of both sexes
573 that share a nest and the same territory (Schradin and Pillay 2005). Similarly, intra-
574 specific variations of gorillas' social organization are influenced by ecological and social
575 factors (Yamagiwa et al. 2003). In addition, hyenas adjust their grouping patterns
576 following a fusion-fission dynamics in response to feeding competition; they are the
577 most gregarious during periods of abundant prey, but forage alone when cooperative

hunting attracts numerous competitors (Smith et al. 2008). Opportunistically solitary individuals may gather in temporary unstable mixed-sex groups. The composition and the stability of these groups differ across habitats and groups tend to be open and ever-changing. For instance, members of aggregations of giraffes (*Giraffa camelopardalis*) usually change every few hours (Leuthold 1979, van der Jeugd and Prins 2000). We inferred that group-living patterns vary with *sexual*, *ecological* and *behavioural* factors as in a mechanism that integrates the characteristics of social systems with individual behavioural strategies and ecological requirements.

EVIDENCE FROM OTTER SPECIES

Group structure changes

Social otters pairs mate for life. As the alpha pair is dominant, offspring of subsequent years frequently stay with their parents, forming extended families and the territories of different groups do not overlap. Indeed, the reasons why females remain in their family group differ from those of males. For instance, North American river otter males are more social than females and to cooperate for feeding so that Blundell et al. (2002a) concluded that cooperative foraging is a key factor influencing social organization of coastal river otters.

Different forms of social organisation can occur even within a species. Group-living otter species present more intraspecific variations than solitary species. By confining ourselves to the concept of 'social species' to understand the evolutionary determinants of group-living life, we underestimate both the evolutionary significance of so-called 'solitary' species, *i.e.* species showing solitary habits (Lodé et al. 2003) and the importance of intraspecific variations and the behavioural plasticity of populations.

603 Therefore, by focusing on the population level rather than only on the species level,
604 analysis of changes in social life can highlight new relevant factors.

605 The group structure of otters changes according to trophic resources and social
606 interactions and group stability differs across different habitats. While Prox and Farine
607 (2020) suspect that tolerance and stability are two central elements of mammalian
608 social organization, it seems that one of these traits is not independent of the other and
609 that stability is promoted by social tolerance. Social life of numerous species seems
610 actually to be organized around the more or less extended family. Thus, although
611 kinkajous generally solitarily (Kays & Gittleman 2001), adult males and females within a
612 group were unrelated while subadults and juveniles were their offspring, suggesting a
613 family structure (Kays et al. 2000).

614 Nonetheless, juveniles can only stay if the parental territory can provide sufficient
615 resources to meet their needs. Actually, otters adjust their grouping patterns in
616 response to food availability, to competition and to predators. It could be reasoned that
617 group-living formations are driven by *sexual, ecological and behavioural variations*
618 reflecting individual decisions and life-history traits, and emphasizing the structural role
619 of social interactions, even for solitary species. Thus, the term 'social life' could be
620 thought to reflect a set of quite different situations (Fig. 3) where each step builds a
621 more or less temporary social organization: *i.e.* 1) *family group*, 2) *extended family*
622 *group*, often with an *alpha dominant pair but with no helpers* 3) *social group with*
623 *helpers*, 4) *collective hunting group* (cooperative activities), 5) *solitary life-style* 6)
624 *unstable mixed-sex group* ('individualistic' foraging) and 7) *male social congregation.* By
625 identifying the main facets of social organization (excluding eusociality), and reflecting
626 more or less dynamic structures according to individual decisions and ecological
627 conditions, this typology of group-living is relevant for numerous species, avoiding
628 imprecise definitions such as subsocial.

629

630 During ontogeny, interactions that define the place of each individual in a group
631 are developed within their *family group*. *Solitary habits* differ from *family group* because
632 offspring stay in their *family group* until they reach sexual maturity, whereas offspring
633 have to leave their mother and disperse soon after weaning when living a *solitary life*.
634 Although animals forage solitarily, they can gather opportunistically in open mixed-sex
635 aggregations (*unstable mixed-sex group*) for some hours or some months in response
636 to predation pressure or to exploit temporary abundant resource. These *unstable*
637 *groups* are mainly composed of females and juveniles, sometimes a *family group* can
638 join an unstable group temporarily. Juveniles in a *family group* disperse when they
639 reach sexual maturity while *extended family groups* include several generations of
640 young. Males may be encouraged to stay within an *extended family group* when
641 competition for trophic resources is quite restricted and when females do not disperse,
642 since their chances to find a mate are then reduced, leading to an *extended family*
643 *group*. Thus philopatry and delayed dispersal would result in sexual competition for
644 mates, involving dominance-subordinate interactions with possible suppression of
645 reproduction (*alpha dominant pair*). Subordinates can be driven to become helpers to
646 facilitate their maintenance within a group forming a *highly social group with helpers*,
647 generally dominated by an alpha pair, although they can have a relationship involving
648 varying degrees of conflict with dominants. Helpers have to participate in the rearing of
649 the progeny but may forage 'individualistically'.

650

651 **Collective hunting and prey switching**

652 *Collective hunting* by otters may occur, in the form of cooperative activities, according to
653 the size and mobility of available prey and could be affected by competition with other
654 predators. Indeed, forming a cooperative group appears an efficient strategy allowing

655 animals to catch rapid prey, often grouped in schools, or prey relatively large in regard
656 to their size, or when competitive interactions with other predators appear unfavourable
657 (Packer and Ruttan 1988). While cooperative breeding could be regarded as an
658 'altruistic' behaviour because helpers contribute care to offspring at the expense of their
659 own reproduction, *collective hunting* characterizes a more selfish behaviour. Packer and
660 Ruttan (1988) provide a simple but operational definition of cooperation as '*hunting in*
661 *the presence of a companion'*. Collective hunting can sometimes be interspecific as for
662 instance coyotes and American badgers. In fact, although *collective hunting* reveals a
663 form of cooperative activities based on long-term relationships (Smith et al. 2012), it can
664 sometimes result in a certain asymmetry of interactions such an unequal sharing of food
665 (Packer & Ruttan 1988, Boesch 1994), the breeding pair typically monopolizing most of
666 food (Mech and Boitani 2003). Boesch and Boesch (1989) recognized different levels of
667 cooperation including coordination and collaboration in hunting behaviour. However,
668 hunting cooperation does not appear to require many deliberate interactions as
669 suggested by subsocial spiders (Wickler and Seibt 1993), so that there is no reason to
670 claim that cooperative hunting reflects advanced cognitive abilities or complex social
671 organizations, since similar strategies are generally used for different prey (Packer and
672 Ruttan 1988, Mech and Boitani 2003).

673 Finally, individuals may disperse, foraging and using a den alone (*solitary life-style*),
674 or can gather opportunistically in unstable mixed-sex aggregation (*unstable mixed-sex*
675 *group*) including mainly females and juveniles, or form single-sex bachelor groups (*male*
676 *social congregations*) depending on ecological resources and predators. Solitary
677 mustelids seem to switch prey (Delibes and Adrian 1987, Weber 1990, Lodé 1996b,
678 1997, Clavero et al. 2003, 2006, Prigioni et al. 2006, Remonti et al. 2008, Pagacz and
679 Witczuk 2010) when they compete with other predators. Depending on prey type and on
680 exploited habitat, solitary habits are favoured by prey switching to alternative resources,

681 whereas specialization in particular prey types could facilitate congregations (Lodé
682 2000, Blundell et al. 2002a). Being aquatic species, otters' capacities to switch prey are
683 limited, ranging from fish to arthropods. Giant otters and Asian small-clawed otters are
684 able to cooperate and coordinate their predatory activities (Schmelz et al. 2017). In fact,
685 feeding specializations and behavioural inertia against prey switching could be linked to
686 the fact that efficient exploitation of distinct prey requires animals to have radically
687 different sensory motor skills to survive. Furthermore, the existence of the unstable rafts
688 of sea otters and of male bachelor social congregations, at least of North American river
689 otters and African clawless otters, suggest that dispersal and competition for mates
690 cannot preclude group-living patterns and cooperation.
691
692 **A series of individual decisions**
693 We propose that group-living is driven by a sequence of individual decisions following
694 *sexual*, *ecological* and *behavioural* covariance (SEB model). Although this model does
695 not discriminate very well among variables, it can also account for the fission-fusion
696 dynamics common to many group-living species. Simple immediate decisions within a
697 family group govern complex social interactions prone to favour reproduction success in
698 the long term. Individuals engage in different optional alternatives in response to more
699 or less proximal factors:
700 *1)* Soon after weaning, an animal can either disperse or stay:
701 *i*) if it disperses, *a)* it can live an solitary life, exploiting a food resource until depletion
702 when resources are distributed in patches, or *b*) it can join opportunistically an unstable
703 mixed-sex group or *c*) it can join a bachelor group when trophic resources replenish
704 rapidly or when it feeds upon large prey, or *d)* it can join another group and mate later,
705 dispersal thus avoids inbreeding depression.

706 *ii*) if it stays and remains in its family group, *a)* it can forage solitarily when good
707 resource availability reduces competition, or *b)* it can hunt collectively when prey are
708 gathered in schools or are too large to be caught alone, or *c)* a family group composed
709 of a female and her cubs can join an unstable group temporarily.
710 *2)* After reaching sexual maturity or when the alpha pair breeds,
711 *i)* it can disperse as in the first option,
712 *ii)* or it can stay and engage more or less subordinate behaviour, and becomes a helper
713 if it is tolerated by the dominant (Fig. 4). Although no genetic tests have yet proven
714 extrapair paternity, it is likely that several adult individuals participate in reproduction,
715 especially in species such as small-clawed otters, American river otters and giant otters,
716 as otters and mink may be capable of superfetation (Yamagushi et al. 2004, Broekhuizen
717 et al. 2007).
718 Habitat features and prey types affect the social organization of otters suggesting
719 that social systems could be associated with particular niche variations. A major reason
720 of group-living can be found in the fact that the trophic resource replenishes rapidly,
721 thus favouring the formation of a group. This is principally the case when invertebrates
722 constitute the main food source. For instance, sea otters feed preferentially upon clams,
723 mussels, sea stars and urchins and lead a very social life. Giant otters opportunistically
724 eat the most abundant species locally and cooperate for hunting big fish and alligators
725 (Rosas et al. 1999). Cape clawless otters' diets include few fish but many crustaceans
726 and molluscs, whereas more solitaries species such as neotropical otters prey on small
727 fish, smooth otters chiefly prey on large fish and Eurasian otters feed mainly on small
728 fish, crayfish and amphibians. As a crab-specialist (Foster-Turley 1992, Kruuk et al.
729 1994, Melish et al. 1996, Kanchanasakha 2007, Hon et al. 2010) small-clawed otters
730 exhibit a high level of social interactions in *highly social groups with helpers,* but are
731 very flexible according to their environment (Perinchery 2008, Hussain et al. 2011,

732 Perinchery et al. 2011, Perdue et al. 2013). It seems that intraspecific competition is
733 considerably reduced because patches of prey cannot be exploited in a single feeding
734 although each group member forages solitarily. Hunting success for such small prey is
735 likely to be dependent on dexterity and locomotor performances. Smooth-coated otters
736 can learn socially how to exploit novel food resources and adopt a 'copy when young'
737 strategy (Ladds et al. 2017). All otters are very agile in water, but because their short
738 claws do not extend beyond their forepaws, small clawed otters have an excellent
739 sense of touch and coordination. Similarly, group-living African clawless otters lack
740 claws and have been observed to feed on crabs, frogs and crayfish thus reducing
741 intraspecific competition (Butler and Marshall 1996, Somers 2000, Parker et al. 2005).
742 Though this species sometimes lives solitarily, African clawless otters can form family
743 groups of up to ten individuals (Butler and Marshall 1996). Similarly, spotted-necked
744 otters do not hunt cooperatively but can live in small family groups in swamps and lakes
745 where this species catches invertebrates, crabs and small fish (Kruuk and Goudswaard
746 1990).

747 Although marine otters mainly exploit molluscs, crustacean and benthic fish along
748 rocky coasts, this species' social behaviour is reduced to a *family group*, and sometimes
749 exhibits solitary habits, probably because this species uses wave-exposed habitats, is
750 very vulnerable to predators and depends strongly on available safe rocky shelters
751 (Villegas et al. 2007, Medina-Vogel et al. 2007, Mangel et al. 2010, Valqui 2011).
752 Smooth-coated otters form monogamous pairs and during the monsoon season their
753 basic *family group* consists of an adult female and offspring, they live in large rivers and
754 swamps but forage in shallow waters for slow fish, frogs, crabs, and insects (Helvoort et
755 al. 1996, Hussain 1996, Perrin and D'inzillo Carranza 2000, Anoop and Hussain 2004,
756 Khan et al. 2010). Group-living giant otters' diet in the flooded rain forest includes chiefly
757 small cichlids (Duplaix 1980, Carter and Rosas 1997, Davenport 2008; Leuchtenberger

758 and Mourão 2008, Davenport et al. 2010), revealing that solitary foraging could diminish
759 feeding competition within highly social groups. Giant otters can prey cooperatively
760 upon some large fish or fish schools, individuals surrounding prey when hunting
761 collectively (Rosas et al. 1999).

762 River otters have broad habitat preferences but while European and North
763 American river otters inhabiting rivers and streams generally exhibit *solitary habits* and
764 opportunistic diets (Melquist and Hornocker 1983, Mason and Macdonald 1986,
765 Newman and Griffin 1994, Kruuk and Moorhouse 1991, Kruuk 1995, Beja 1996; Durbin
766 1998, Ludwig et al. 2002, Bifolchi and Lodé 2005). European otters appear to be more
767 social than previously thought (Quaglietta et al. 2014) and most otter species can
768 present flexible social behaviours. Sociality is related to habitat features and acquisition
769 of food so that both North American river otters and European otters exploiting rocky
770 coasts and small benthic fish can live in groups (Kruuk and Moorhouse 1991, Shannon
771 1991, Rock et al. 1994, Reid et al. 1994, Larivière and Walton 1998, Blundell et al.
772 2002a, Blundell et al. 2004, Cote et al. 2008).

773 Although exploiting the same resource can increase competition dramatically,
774 larger groups of North American river otters coincide with increased availability of
775 schooling fish, because a large number of individuals surround schools in cooperative
776 hunting (Blundell et al. 2004). Conversely Neotropical river otters, southern river otters,
777 and Congo clawless otters have been observed to exhibit solitary habits when prey is
778 dispersed in patches, exploiting linear wooded freshwater brooks, rivers and lakes
779 (Helder and De Andrade 1997, Pardini 1998, Angelici et al. 2005, Kasper et al. 2004,
780 Kasper et al. 2008, Sepulveda et al. 2009, Gomez et al. 2010, Rheingantz et al. 2011).
781 Although this is probably the case for some other otter species, sea otters are known to
782 form opportunistically *bachelor congregations* and *mixed-sex unstable groups* called
783 pelagic raft, including from a dozen to as many as a thousand individuals mainly

because they are exposed to marine predators (Garshelis et al. 1984). However reproductive adult males remain territorial and exclusive (Riedman and Estes 1990, Pearson and Davis 2005). Sea otters are clam-specialists but show individual dietary patterns transmitted along matrilines mediating prey specializations and intraspecific competition (Monson et al. 2000, Estes et al. 2003, Johnson et al. 2009, Laidre et al. 2009).

CONCLUSION

Despite decades of research dealing with group-living among species, we are far from understanding the evolution of the social life of animals, maybe because it is unlikely that any one model can explicate all facets of sociality.

Social factors rather than ecological factors may play an important role in the formation and cohesiveness of groups in otter species. There is however much evidence that ecological factors and other habitat constraints limit dispersal and promote group-living. Variations of social life style actually reveal a series of events which give rise to individual decisions in cascade related to ecological factors, otters adjusting social patterns to environmental variations. Simple immediate decisions govern complex social interactions driving group-living and favouring future reproduction success. Originating from mother-cub relationships, the flexible social lifestyles of otter species can reduce the cost of sociality because individuals can avoid social interactions when benefits are low whereas they can gather together when group-living provides more advantages.

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1337

1338 **Table I.** Social traits of 14 otter species. Family structure refers to pairs, social structure
1339 refers to extended family and highly social structure refers to groups including
1340 helpers.

Species		**Habitat**	**Lifestyle**	**Parental investment**
Congo clawless otter	*Aonyx congicus*	fresh rivers, ponds, marshes, lakes	solitary	female
Neotropical river otter	*Lontra longicaudis*	rivers, lakes, small streamlets, coast, lagoons	solitary	female
Hairy-nosed otter	*Lutra sumatrana*	fast flowing rivers, peat swamp, streams, mountain rivers	solitary	female
Japanese otter (Extinct)	*Lutra nippon*	fresh rivers, ponds, marshes	solitary	female
Southern river otter	*Lontra provocax*	fresh rivers, ponds, marshes	solitary	female
Spotted necked otter	*Lutra maculicollis*	lakes, large rivers	solitary or family group	female
Marine otter	*Lontra felina*	rocky coasts and seashores	family group, but sometimes solitary	pair
Smooth coated otter	*Lutrogale perspicillata*	large forested rivers, swamps	solitary or family group	female
European otter	*Lutra lutra*	fresh water ecosystems and rocky coasts	mostly solitary, sometimes social	female
Cape clawless otter	*Aonyx capensis*	marshes, rocky coasts and seashores, mangrove	solitary, family group or social	pair

Sea otter	*Enhydra lutris*	oceanic kelp forests	social	female or pair
Giant otter	*Pteronura brasiliensis*	Large low rivers, flooded rain forest, mangroves	highly social	helpers
North American river otter	*Lontra canadensis*	fresh rivers, low rivers, ponds, lakes, marshes, rocky coasts	solitary, family group or highly social	helpers
Oriental small-clawed otter	*Aonyx cinerea*	large forested rivers, swamps, mangroves	family group or highly social	helpers

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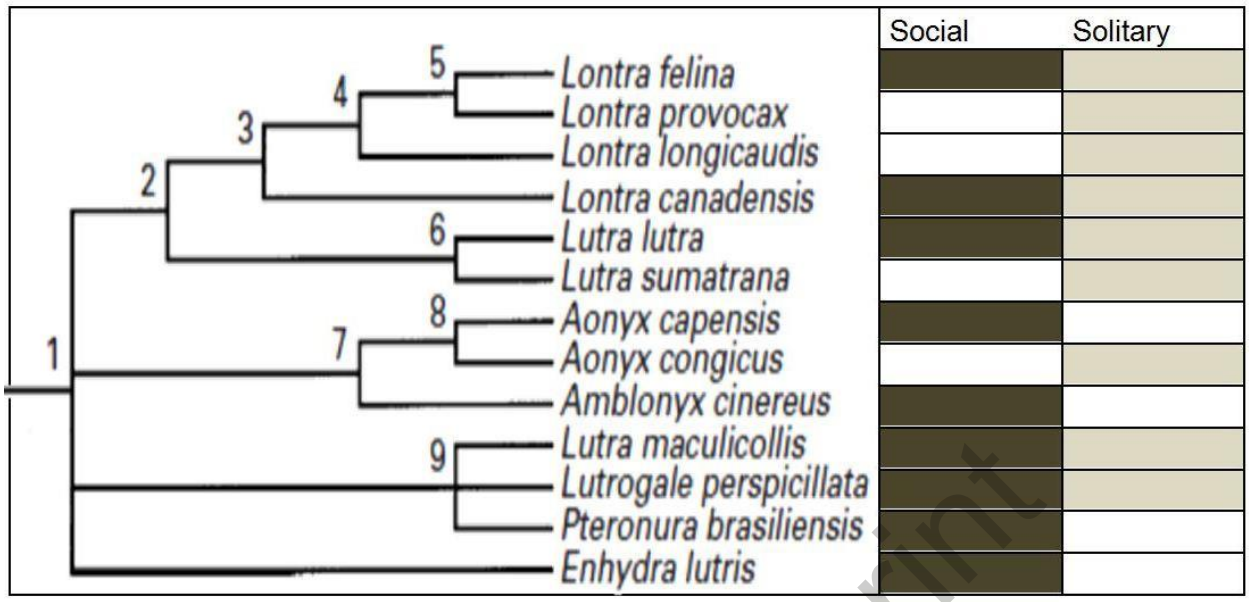
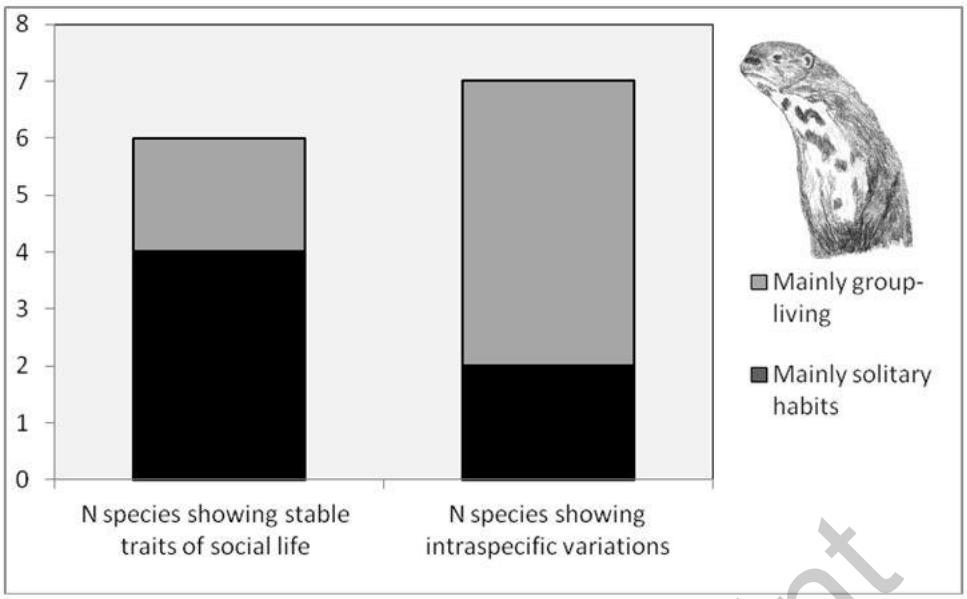


Fig. 1. Phylogenetic relationships evaluated by a super-tree construction (maximum parsimony, maximum likelihood and Bayesian inference methods, from Bininda-Edmonds et al. 1999; Koepfli et al. 1998 and Koepfli et al. 2008) related to social life characteristics for 13 otter species: marine otter (*Lontra felina*), southern river otter (*Lontra provocax*), neotropical river otter (*Lontra longicaudis*), North American otter (*Lontra canadensis*), European otter (*Lutra lutra),* hairy-nosed otter *(Lutra sumatrana),* African clawless otter *(Aonyx capensis*), Congo clawless otter (*Aonyx congicus),* small-clawed otter (*Amblonyx*/*Aonyx cinerea*), spotted-necked otter *(Lutra maculicollis*), smooth-coated otter (*Lutreogale perspicillata*), giant otter (*Pteronura brasiliensis*) and sea otter (*Enhydra lutris*). (Nodes 1-9 are numbered with bootstrap and posterior probabilities).



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1358 **Fig. 2.** Intraspecific variations of otters' social structures. European otters (*Lutra lutra*),
1359 spotted necked otters (*Lutra maculicollis*), smooth-coated otters (*Lutrogale*
1360 *perspicillata*), North American otters (*Lontra Canadensis*), marine otters *(Lontra*
1361 *feline*), small-clawed otters (*Aonyx cinereus*) and African clawless otters *(Aonyx*
1362 *capensis*) (54% of the studied species) present intraspecific variations whereas
1363 Congo clawless otters (*Aonyx congicus*), giant otters (*Pteronura brasiliensis*), hairy-
1364 nosed otters (*Lutra sumatrana*), neotropical river otters (*Lontra longicaudis*), sea
1365 otters (*Enhydra lutris* and, southern river otters (*Lontra provocax*) (46%) present
1366 stable social organizations.

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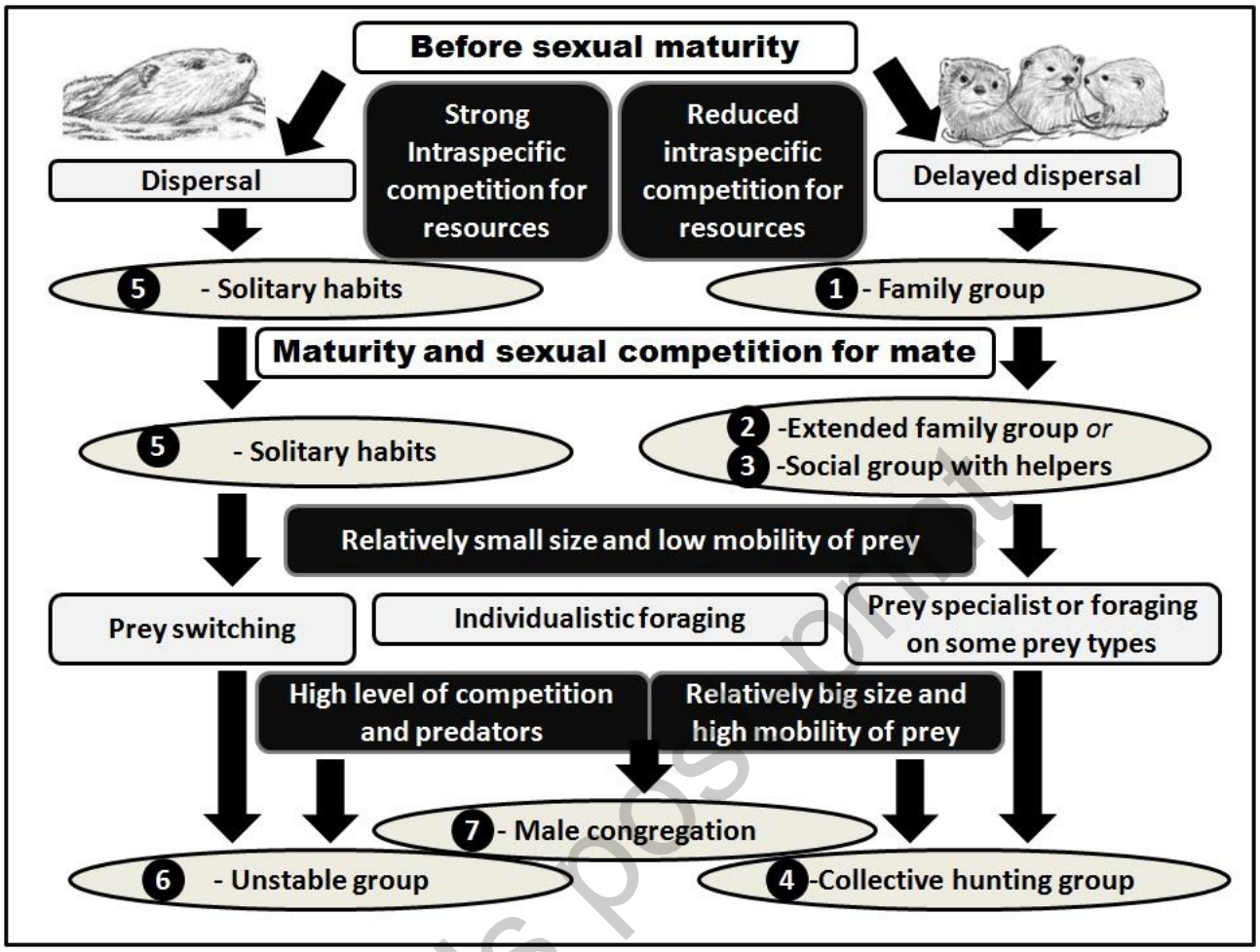

Fig. 3. Schematic representation of the socio-ecological predictions for otters' social organization (SEB covariance model). White text on black: ecological factors influencing social decisions; grey background: life style. Black circles: social life types: **1**) *family group* (offspring disperse when they reach sexual maturity); **2**) *extended family group*, often with an alpha dominant pair (several generations cohabit); **3**) *social group with helpers*, generally with an alpha dominant pair; **4**) *collective hunting group;* **5**) *solitary life-style* (offspring disperse soon after being weaned); **6)** *mixed-sex unstable group* and **7**) *male social congregations.*

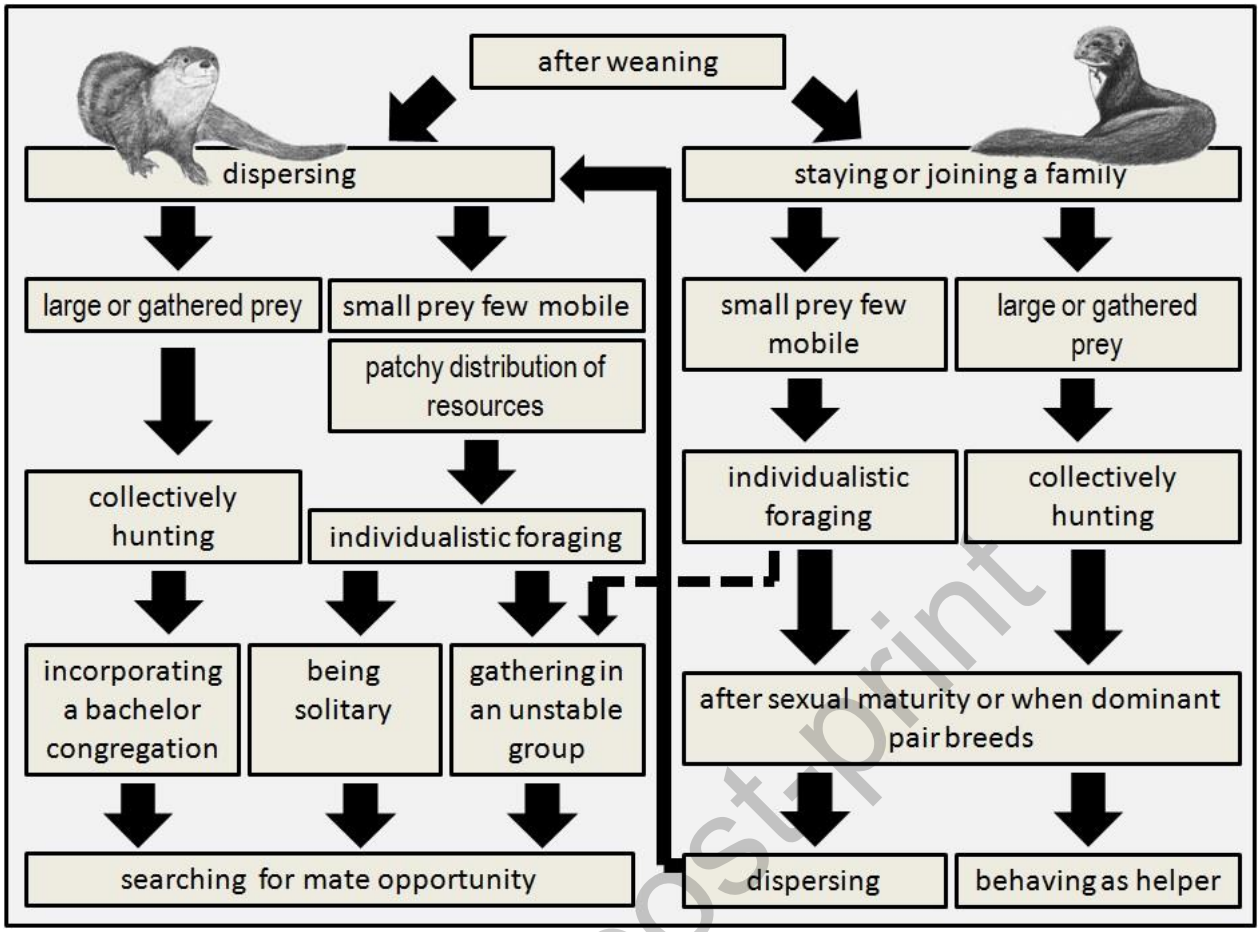

Fig. 4. Sequence of individual step-by-step decisions following *sexual*, *ecological* and *behavioural* covariance in otter species in which each step builds a more or less temporary social organization. Individual otters have to make a number of decisions after weaning: to disperse, to forage solitarily, to remain solitary or to join opportunistically an unstable mixed-sex group or a bachelor group. If it remains in its family group, it can forage either individualistically or collectively according to prey type; sometimes, a family group can join an unstable group temporarily. When the alpha pair breeds, offspring may disperse as in the first option or stay and behave as a subordinate helper, if it is tolerated by the dominant.