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Abstract

Fission-fusion dynamics describe animal social systems that are fluid and characterized by varying group sizes. Costs and benefits associated with grouping are considered to be the driving force for separation (fission) and joining (fusion) of individuals, resulting from ecological (e.g., food availability, predator abundance) and social (e.g., behavioral state, presence of calves) factors. The behavioral state gives insights into an animal's ecology and allows protection of the species or population. The present study investigates which factors influence behavioral state and fission-fusion dynamics in common dolphin (*Delphinus delphis*) groups with calves in the south of Portugal. Between June and October of 2016, 2017 and 2019, 39 focal follows based on unmanned aerial vehicles (UAVs) were conducted, resulting in 768, 30-second behavioral samples (384 minutes). A multinomial model based on generalized estimating equations framework was used to model: i) the behavioral state by testing the responses to group size, total number of calves and month; ii) and fission-fusion dynamics assessing the effect of behavioral state, month, total number of calves and time of the day. The behavioral state of dolphin groups with calves was statistically significantly affected by the total number of calves and month. As the number of calves increased, *resting* behavior was less likely to occur than *travelling* (OR = 0.7, p = 0.015). Dolphin groups with calves were less likely to be *socializing* in *July* than to *travel* in *June* (OR = 0.1, p = 0.021). Group size had no statistically significant influence on the behavioral state in the present study. This study also revealed, that common dolphins in the south of Portugal exhibit a high rate of fission-fusion dynamics, but were not influenced by the factors considered in this study (i.e., behavioral state, month, total number of calves and time of the day). By assessing behavior and fine-scale social dynamics in common dolphins, this study enhances the current understanding of ecological and social aspects shaping grouping patterns and behavior in common dolphin groups with calves. This study also highlights the advantages of using unmanned aerial vehicles (UAVs) to assess behavioral data in wild animals.

Keywords: Behavior · Cetacean · Calves · Social structure · Grouping patterns · Unmanned aerial vehicles

Resumo

A organização de indivíduos em grupos é comum nos mamíferos e a maioria das espécies apresentam comportamento social durante o período de reprodução e cuidados parentais. Os laços sociais entre indivíduos que partilham o mesmo ambiente podem ter impactos sobre os próprios e sobre a sobrevivência da descendência. O termo fissão-fusão (FF) foi inicialmente utilizado para descrever o sistema social dos primatas que alteram o tamanho do grupo frequentemente e dividem-se em subunidades. A dinâmica da fissão-fusão descreve, portanto, sistemas sociais são fluidos e caracterizados por tamanhos de grupo variáveis. Os custos e benefícios associados ao agrupamento são considerados a principal razão para a separação (fissão) e união (fusão) de grupos, provavelmente provenientes de factores sociais (e.g., estado comportamental, presença de crias) e ecológicos (e.g., disponibilidade de alimento, presença de predadores). Por exemplo, diferenças na distribuição espacial e temporal de recursos alimentares podem favorecer padrões de associação flexíveis, para reduzir a competição intra-específica e aumentar a possibilidade de explorar novos recursos. Em troca, associações mais coesas e estáveis podem ser formadas com o objetivo de maximizar a defesa contra predadores. Assim, o risco de predação pode favorecer a agregação de indivíduos em locais de descanso comunitários durante a noite, que posteriormente se dividem em pequenos grupos durante o dia para alimentação. Adicionalmente, a dinâmica de fissão-fusão pode ser influenciada pelo sexo, idade e/ou fase reprodutiva dos indivíduos. Em algumas espécies, os machos podem apresentar taxas de fusão mais elevadas a fim de cooperarem com indivíduos relacionados e impedir o acesso às fêmeas por machos de grupos vizinhos. As dinâmicas de fissão-fusão são comuns em algumas espécies de primatas, elefantes, hienas malhadas e golfinhos. O estudo da socialidade e comportamento em mamíferos pode fornecer informações importantes sobre a sua evolução e fornecer informação relevante para a proteção das espécies, especialmente as ameaçadas de extinção.

Os cetáceos são mamíferos marinhos de maturação lenta e uma expectativa de vida longa. Este grupo de organismos vive a maior parte da sua vida debaixo de água, o que torna particularmente difícil o estudo dos seus sistemas sociais e comportamentos. Entre os cetáceos, existem grandes variações inter- e intra-específicas na organização social, desde ligações sociais estáveis e duradouras (e.g., orcas, cachalotes, cachalotes, baleias-piloto de barbatanas longas) a sociedades fluidas com uma elevada dinâmica de fissão-fusão (e.g., golfinho riscado, golfinhos-roaz, golfinhos de risso). Estudos recentes identificaram como factores ambientais e sociais que afetam a dinâmica de fissão-fusão o comportamento, sexo, grau de parentesco, sazonalidade e pressões antropogénicas.

Veículos aéreos não tripulados (UAV), vulgarmente conhecidos como "drones", são uma tecnologia inovadora e que tem vindo a sofrer um rápido desenvolvimento nos últimos anos. Geralmente, os UAV podem ser distinguidos em dois tipos: 1) UAV de asa fixa (FW) e 2) UAV de descolagem e aterragem verticais (VTOL). A funcionalidade dos sistemas VTOL é comparável à dinâmica dos helicópteros. A maioria dos modelos usa 4 a 8 rotores que permitem que a aeronave paire em uma posição estacionária, permaneça em baixas altitudes, mova-se lentamente e permita decolagens e aterragens verticais, eliminando a necessidade de uma pista. Além disso, os modelos comerciais incluem câmeras de alta definição integradas com estabilizadores de imagem mecânicos (ou seja, Gimbal), permitindo que o piloto capture vídeos e/ou fotos em alta qualidade de uma perspectiva vantajosa. Além disso, os VTOLs são geralmente leves (< 5 kg), portáteis, económicos e prontamente disponíveis em vários fabricantes comerciais. No entanto, tais sistemas requerem controle ativo por um piloto remoto e sua distância máxima de voo é limitada a uma faixa de dezenas de quilómetros, enquanto a vida útil da bateria de cerca de 30 a 45 minutos permite apenas tempos de transmissão bastante curtos em áreas de pesquisa menores em comparação com FWs. As características avançadas dos modernos UAV VTOL torna-os versáteis para várias aplicações, incluindo a investigação de vida selvagem, incluindo estudos de comportamento e populacionais, recolha de amostras biológicas, monitorização e estudo de habitat. O sucesso dos UAV neste campo pode ser explicado pela diversidade dos modelos existente e pelas suas inúmeras formas de funcionamento, ao mesmo tempo que continuam a ser sistemas rentáveis e eficazes na colheita de dados sistemáticos e de alta resolução (temporal e espacial). Apesar das numerosas vantagens do uso de veículos aéreos não tripulados para a investigação da vida selvagem, a tecnologia tem limitações e pouco se sabe sobre os impactos que os UAV podem causar nos animais selvagens. As diferentes populações de uma espécie podem apresentar respostas idiossincráticas à presença de um UAV, dependendo de fatores tais como a espécies, fase de vida, habitat, condições ambientais tipo de UAV bem como, o método de operação (por exemplo, ruído emitido, velocidade, distância). Considerando as espécies de pequenos cetáceos (p. ex., delfinídeos), as respostas comportamentais como reacção a um UAV que se aproxima, permanecem pouco investigadas. Contudo, as provas actuais indicam que os UAV voando a baixas altitudes nas proximidades de diferentes espécies de golfinhos desencadeiam respostas comportamentais a curto prazo dos animais.

O presente estudo investiga quais os fatores que influenciam o estado comportamental e a dinâmica de fissão-fusão em golfinhos comuns (*Delphinus delphis*) em grupos com cria no Sul de Portugal. Entre Junho e Outubro de 2016, 2017 e 2019, foram realizadas 39 amostras focais

usando UAV, resultando num total de 768 amostras comportamentais tendo por base intervalões de 30 segundos (384 minutos). Utilizando equações de estimativa generalizada, modelou-se: i) o estado comportamental, testando as respostas ao tamanho do grupo, número total de crias; ii) e a dinâmica de fissão-fusão em função do estado comportamental, mês, número total de crias e hora do dia. As variáveis mês e número de cria mostraram ter um efeito significativo no estado de comportamento dos grupos de golfinhos com cria. Com o aumento do número de crias, o comportamento de repouso foi significativamente menos provável de ser observado do que o de viajar. Por outro lado, a probabilidade de avistar grupos com cria a descansar no mês julho foi significativamente inferior à probabilidade de observar grupos a viajar em Junho.

Este estudo revelou que os golfinhos comuns com crias no Sul de Portugal, apresentam uma elevada taxa de dinâmica de fissão-fusão, mas não foram observados efeitos significativos do estado comportamental, número total de crias e hora do dia na dinâmica de fissão-fusão, exceto para a variável mês.

A avaliação do comportamento e a dinâmica social de grupos de golfinhos comum com cria permitiu uma melhor compreensão dos aspetos ecológicos que influenciam os padrões de agrupamento e comportamento deste animais. Adicionalmente, este estudo demonstra que a utilização de veículos aéreos não tripulados (UAV) pode ser uma mais valia para o estudo comportamental de animais selvagens pela sua eficácia e qualidade dos dados recolhidos.

Palavras-chave: Comportamento - Cetáceos - Crias - Estrutura social - Padrões de agrupamento - Veículos aéreos não tripulados

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List of Abbreviations

UAV	–	unmanned aerial vehicle
FW	–	fixed wing
VTOL	–	vertical take-off and landing
FF	–	fission-fusion
FI	–	fission
FU	–	fusion
ST	–	stable
F	–	foraging
R	–	resting
S	–	socializing
T	–	travelling

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1. General Introduction

1.1 Sociality in mammals

The behavioral ecology theory suggests, that sociality will evolve when the benefits of associations between conspecifics exceeds the costs[1]. In mammals, sociality is widespread and most species are social during the reproduction period and parental care, at the least[2]. Nevertheless, social bonds between individuals that share the same spatiotemporal environment don't only occur during reproduction and parental care, and may have impacts on their own and their offspring's survival[3–5]. Factors like food availability and distribution, predation risk and gender segregation can alter the social structure of a species or population[6]. Studying sociality of mammals may provide important information on their evolution and may increase our knowledge in an effort to protect endangered species.

Cetaceans are slow reproducing, long-lived marine mammals that are known to spend most of their life beneath the ocean's surface[7], making it particularly difficult to successfully investigate their social systems and behaviors. Nevertheless, recent studies could reveal how environmental and social factors such as behavior, gender, kinship, individual personality, season and anthropogenic pressures may result in varying association patterns of cetacean taxa[8–14].

Genetic analyses may give insights into the social organization of delphinid species. In a genetic study by Viricel et al. (2008) mitochondrial and nuclear markers from common dolphins (*Delphinus delphis*) that were subject to a mass-stranding event on the English Channel coast, were analyzed and then compared to single stranding events of the same species on the French Atlantic coast in order to examine similarities or differences between those events[15]. Both groups showed similar high degrees of haplotype diversity and mtDNA data did not consist with a matriarchal social structure[15], a finding that is contradicting to the results of Amos (1999) who suggested matrilineal social systems for common dolphins[16]. The non-significantly different relatedness values between the mass-stranded pod and the single strandings suggest, that individuals from the mass-stranding were mainly composed by unrelated individuals[15]. Data derived from both marker systems revealed no strong family structure except for two mature females and one mother-calf pair, indicating that kin associations were not likely to be a driving factor for the grouping pattern of the pod[15]. However, the composition of the pod was characterized by non-related females that shared the same reproductive stage, which is a similar finding to another mass-stranding event of 12 common dolphins in New Zealand using the same genetic methods[17]. Female-calf dominated groups are hypothesized to segregate in habitats with enhanced resource availability and decreased predation pressure[18], while avoiding male harassment due to strong sperm competition during the mating period[19].

The social structure may alter numerous properties of a species such as ecology, behavior, genetic diversity, disease transmission and fitness, making it crucial to understand the sociality of species and populations in order to efficiently conserve them[4,20–22].

1.2 Fission-fusion dynamics

1.2.1 General explanation of the concept

First implemented by Hans Kummer (1971), the term "fission-fusion" was used to describe the social system of primates that would change their group size and split into subunits in reaction to both, their activity and the distribution and availability of resources[23,24]. Hence, the extent of variation in individual membership and the spatial cohesion of a group over time may be referred to as "fission-fusion dynamics"[25]. Although fission-fusion (FF) dynamics are rare amongst the social systems of mammals, they are yet typical for some primate species[26], elephants[27], spotted hyenas[28] and dolphins[7]. Any animal society may be characterized by its degree of fission-fusion dynamics, which can range from highly fluid (flexible membership) to highly cohesive (stable membership)[25]. Social systems are being influenced by the spatio-temporal variations in grouping patterns, since they influence the likeliness for individuals to interact with each other[25]. Aureli et al. (2008) proposed three dimensions of fission-fusion dynamics: 1) The temporal variation in spatial cohesion among group members, 2) the temporal variation in party size and 3) the temporal variation in party composition (*Figure 1.1*)[25]. Assessment of data for the three dimensions allows to place different species as well as populations of a species within multidimensional fission-fusion models, to investigate the qualitative and quantitative differences of fission-fusion social systems with regards to cognitive abilities, social interactions and socioecological interactions[25].

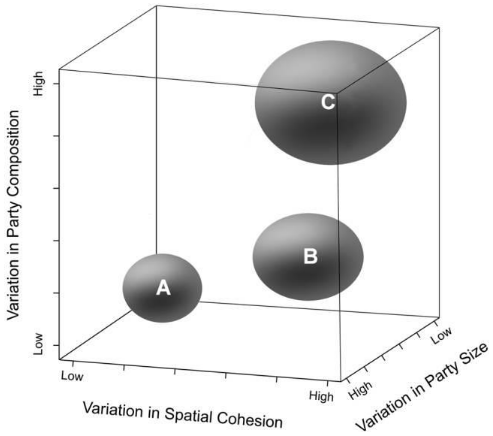

Figure 1.1: Three-dimensional conceptual framework illustrated by Aureli et al. (2008) to represent the degree of fission-fusion dynamics of groups and taxa. Region A: low in all dimensions (e.g., very cohesive groups; constantly dispersed situations); Region B: highly variable in spatial cohesion and party size but not in party composition; Region C: high in all three dimensions (highly fluid communities with highly variable party membership). Adapted from Aurelia et al. (2008).

Association patterns of individuals within a species or population are thought to be a response to numerous social and ecological factors in order to maximize benefits (e.g., increased access to food and potential mates, decreased predation risk) and minimize costs (e.g., competition for food and mates, risk of disease transmission) of grouping[6]. Accordingly, patchily distributed and temporally varying food resources may favor flexible association patterns, to reduce intra-specific competition and increase the chance of exploring new resources[29,30]. In return, more cohesive and stable associations may be formed in order to maximize predator avoidance when food resources are plentiful. Moreover, not only food resources but also sleeping sites and the availability and distribution of water holes may influence the social characteristics of free-ranging animals. Such dynamics vary in time depending on the species or population and environmental factors. For example, the risk of nocturnal pressures may favor the aggregation of individuals at communal sleeping sites during the night, whereas aggregations are forced to be divided into smaller foraging parties during the day if food resources are patchily distributed[29,31]. Additionally, fission-fusion dynamics may be influenced by gender, sex, age and/or reproductive stage of individuals. Male individuals of some high-FF taxa are known to cooperate with related males in order to defend access to females against male individuals from neighboring groups[32,33]. In return, events like those could force maturing females to disperse[34,35].

1.2.2 Fission-fusion dynamics in cetaceans

Among cetaceans, there are strong inter- and intra-specific variations of social structures[36]. Their social characteristics range from stable and long-lasting social bonds (e.g., killer whales, sperm whales, long-finned pilot whales) to fluid societies with fission-fusion dynamics (e.g., striped dolphins) and those of both extremes (e.g., bottlenose dolphins, risso's dolphins), likely depending on trade-offs between the costs and benefits of associations with regards to food availability, predation risk or gender specific interactions (e.g., male harassment)[6,37]. Although scientific literature on the social structure of most cetacean species is scarce[38–41], several studies indicate that the main drivers for fission-fusion dynamics are based on the availability and distribution of food resources[42–44], predation pressure[36,43,45,46], kinship[38,42] and gender[38,43,47,48].

1.2.3 Fission-fusion dynamics in dolphins (delphinidae)

The family Delphinidae (dolphins) composed of 40 species represents the most widespread and diverse of all cetacean families[49]. and is characterized by large variations in ecology and social structures[50]. It has been suggested, that the different patterns of social organizations between and within dolphin species may be due to variable availabilities and distributions of food resources and predation risks[45,50]. For example, bottlenose dolphins (*Tursiops truncatus*) exhibit a high degree of fission-fusion dynamics which is thought to be a response to both, food availability and predation risk. When food resources are patchy and limited, bottlenose dolphins are likely to fission into smaller foraging groups in order to minimize intraspecific food competition and to enhance the likeliness of exploring resources, while merging into larger groups when resources are plentiful to increase the dilution effect for a minimized individual predation risk[7,51].

Killer whales (*Orcinus orca*) are a very social delphinid species that are known to hunt in cooperation with close family members, making them apex predators in their habitats[52]. The social structure of killer whales is known to be primarily matrilineal and commonly the species lives in stable groups[53–55]. In the near-shore waters of the Galápagos Islands, killer whales are one of the most frequently sighted cetaceans with most observations occurring during the cold season from July to December[56]. Previous studies found, that populations around Galápagos tend to have an opportunistic feeding behavior with varying prey items such as sharks, fish, turtles, sea lions, whales and dolphins[57–59]. In contrast to most observed killer whale populations around the world, data from a study carried out by Denkinger et al. (2020) indicates that the killer whales of Galápagos live in social organizations more similar to fission-fusion societies, forming rather loose than stable groups[52]. In the same study, the authors found that the average group size consisted of around four animals, which according to Baird and Dill (1996) represents the energetically most efficient number of individuals of transient killer whales living in highly productive and cold environments[60]. Furthermore, killer whales feeding on marine mammals are known to live in small groups[61]. However, bigger groups of the species have been observed hunting large marine mammals such as sperm whales (25 individuals)[62] and baleen whales in Galápagos (5 – 10 individuals)[57]. It is assumed, that large groups may consist of temporary associations formed by multiple pods in order to successfully attack large prey[52]. The waters around Galápagos represent a very variable habitat with dramatic seasonal changes in productivity, that are even more intense during years of the 'El Niño' and 'La Niña' phenomena[63,64]. The seasonality might be a driving environmental factor for the rather unusual variable social structure of groups and the association of different pods in Galápagos[52], compared to killer whales in cold latitudes with stable environments where stable associations are more characteristic[65,66]. However, Galápagos killer whales are not the only populations of the species showing fission-fusion like societies. Transient killer whales off British Columbia, Canada form small foraging groups when feeding on small prey (e.g., seals) whereas larger groups are formed when hunting large prey, such as cetaceans or steller sea lions (*Eumetopias jubatus*)[61].

Comparative studies of delphinid species may give insights into the evolution and aspects of social characteristics within the given habitat and ecology[67]. A study from Parra et al. (2011) compared the social systems of two dolphin species: the Australian snubfin dolphin (*Orcaella heinsohni*), which is the only known cetacean species endemic to Australian and New Guinean waters[68] and the Indo-Pacific humpback dolphin (*Sousa chinensis*), that ranges from the east of South Africa to the north of Australia[69]. Both species are medium-sized animals inhabiting shallow waters in coastal-estuarine areas[68,70], that frequently occur throughout the subtropical and tropical areas of Queensland, Australia[70,71]. The study focused on Cleveland Bay, where ranging patterns of both species were found to overlap while showing similar preferences for habitat selection[72]. Although the two species prefer shallow waters in coastal-estuarine systems, snubfin dolphins appear to occur in shallower waters as well as seagrass meadows and range move closer to river mouths than humpback dolphins[72]. The only known predators for both species are bull sharks and tiger sharks[73], which are rather uncommon in Cleveland Bay and inhabit deeper waters, hence out of range for the dolphin species[72]. Analyses of scars from shark attacks on both species have revealed a low predation risk for both species and that neither species is more likely to be attacked than the other[67]. Stomach content analyses indicated that both species feed on various estuarine fish species with snubfin dolphins additionally feeding on cephalopods (e.g., mainly cuttlefish and squid species)[74,75]. While the abundance of estuarine fish species found in Cleveland Bay shows high spatio-temporal variations[76–78]. cuttlefish and squid are characterized by stable populations with high abundances throughout the year within the whole area[79,80]. Hence it was suggested, that food resources are more available and reliable for snubfin dolphins than for humpback dolphins[67]. The study on both species revealed, that snubfin dolphin groups were generally larger and more stable in their size than groups of humpback dolphins, while individuals of both species associated non-randomly with their conspecifics[67]. However, snubfin dolphins showed stronger associations between individuals that were long-lasting[67]. Humpback dolphins seemed to have less temporally stable associations with their conspecifics, that were described as “casual acquaintances” by the authors[67]. The formation of groups in wild animals is often suggested to result from trade-offs between feeding competition and predation risk[45,50]. Living in smaller groups may be beneficial if food resources are scarce and predation risk is low, whereas larger groups are thought to be favored when predators are abundant and food is plentiful and available. Since the predation risk for both dolphin species in Cleveland Bay was shown to be equally low, it appears unlikely to be the reason for the different social structures and dynamics between the species[67]. It is rather likely, that the different availabilities and distributions of preferred food resources could explain the contrasting group sizes and fission-fusion dynamics of both species[67]. The variable group sizes of humpback dolphins may be an adaption to patchily and unpredictably distributed food resources within the habitat, favoring smaller foraging groups when resources are scarce and larger groups when resources are plentiful in order to minimize intraspecific feeding competition[67]. The suggestion is further supported by behavioral observations: humpback dolphins were likely to forage behind fishing trawlers for long time periods, which are known to be stable and large resources of food[81]. In those events, humpback dolphins aggregated together to form schools that were significantly larger while foraging behind the trawlers in comparison to foraging events independently from trawlers[67]. Ultimately, this would indicate that resource limitation constraints school size of humpback dolphins in Cleveland Bay. On the other hand, snubfin dolphins rely on much more stable food resources through space and time (e.g., fish and cephalopods)[79,80]. Hence, the availability of prey allows for stable and larger groups of individuals[67].

Bottlenose dolphins (*Tursiops truncatus*) are generally characterized by temporal fluid fission-fusion dynamics with individuals joining or leaving a group on a scale between minutes to hours[82,83], while on the other hand individuals are known to form permanent associations with individuals that share the same sex or reproductive stage[82,84]. Mother-calf pairs of bottlenose dolphins associate closely with other mother-calf pairs or females of the same reproductive condition, which is suggested to provide better protection from predation of calves[85]. Altmann (2000) indicated, that mothers who increase the interactions of their offspring with individuals of both sexes, enhance the likeliness of having playmates for the offspring and decrease the risk of predation or infanticide by having more associates that share the same reproductive stage[46]. A bottlenose dolphin mother and its calf are usually closely associated until the calf reaches independency at three to four years of age, or until a new calf is born[82,86]. Such close mother-calf relationships have various advantages: the calf is able to explore and socialize with conspecifics around its mother, it can nurse, learn feeding strategies and habitat use while being protected by the mother and, additionally reduces its energy expenditure required for swimming due to the mothers' drafting hydrodynamics[87]. Despite the benefits of close associations between mothers and calves, there are frequent cases in which mother-calf pairs separate temporarily[85]. Such temporary separations may have benefits for both, mother and calf. While the mother may have increased foraging success by being able to feed uninterruptedly, the calf may increase its independency by gaining social and hunting experience[7,88]. Association between calves may be a determining factor for their individual preference for relationships in adulthood. Male calves or juveniles that frequently associated with each other are sometimes likely to form close bonds with the same male individuals when becoming adult[82,89]. However, separations in which calves were alone were significantly shorter than in cases in which calves were associated with conspecifics[85]. Nevertheless, in mother-calf separation events other mothers were usually in close proximity to calves of associated females which in return provided a certain degree of protection[85]. The habitat type may be an important factor in determining sociality of mother-calf pairs. In Sarasota Bay, Florida the deep waters are dominated by pelagic schooling fish species whereas the sea grass meadows and mangroves in the shallow waters are characterized by demersal fish species[90]. Large schools of fish provide enough resources for large and close associations of bottlenose dolphins in deeper waters, while demersal fish species that do not form schools favor rather loose associations and smaller dolphin groups as a result of the limited food availability[85].

Delphinid species may exhibit association patterns driven by the gender and kinship of individuals as indicated for bottlenose dolphins (*Tursiops spp.*)[43]. In Eastern Australia, female *Tursiops aduncus* have been found to form associations preferably with related females[13,91]. On the other hand, it has been indicated that there is a high frequency of male associations between individuals of *Tursiops truncatus* in the Bahamas[92].

1.2.4 Fission-fusion dynamics in the study species: the common dolphin (*Delphinus delphis*)

The most abundant cetacean species in South Portugal is the common dolphin (*D. delphis*) and yet, little is known about its ecology and social characteristics[93–95]. The primary food resource of common dolphins within the region is a wide variety of fish species forming pelagic schools off the coast, with *Sardina pilchardus* being the preferred prey whose abundances and distributions underly annual fluctuations[96–98]. Potential predators for the delphinid species are killer whales[99] and numerous shark species[100–102]. Castro et al. (2022) investigated, how the presence of mother-calf pairs, the behavioral state and temporal variability may influence fission-fusion dynamics of common dolphins in the South coast of Portugal. Additionally, the behavior and degree of fission-fusion dynamics were tested in response to the presence of mother-calf pairs and time of the day. The authors found that all these factors affected the grouping size of the species[103]. More stable, less social and larger groups were characteristic for cases in which mother-calf pairs were present, with the presence of mother-calf pairs being the main factor in determining fission-fusion rates, behavioral state and group size[103]. Consistent previous studies, Castro et al. (2022) indicated predator protection, offspring socialization and the defense from male harassment as possible explanations for those findings[103]. Larger parties provide enhanced predator protection considering the dilution effect, being beneficial for the increased predation risk of mother-calf pairs[51,104,105]. In contrast, group size decreased during resting periods of common dolphins in South Portugal, which may be an anti-predator strategy in which smaller, cryptic groups are formed to decrease detectability[106]. However, predation risk within the region is thought to be relatively low for common dolphins which may be another reason for frequently observed small group sizes when resting[103]. Similar to the dilution effect of large groups to decrease predation risk, female common dolphins were suggested to use the same strategy in order to decrease male harassment by aggregating with other females of the same reproductive condition[107]. The presence of mother-calf pairs in socializing groups was lower than for groups that did not show social behavior, which is likely to be another strategy of females to avoid male harassment[45,108–111]. For common dolphins in the South of Portugal, foraging did not significantly affect group size[103]. Those findings indicate, that feeding competition is not among the factors influencing fission-fusion dynamics in the species[103]. Castro et al. (2022) found, that common dolphins were more likely to forage (than travel) in June than in September and October, which is likely to be linked with seasonal changes of prey availability within the region caused by peaks in primary production during spring and summer months in South Portugal[112]. In contrast, resting behavior was more likely to be observed during the month of September compared to June[103], which is suggested to be linked with seasonal changes of predator abundance[51] and anthropogenic pressure from tourism peaks during summer[113]. Additionally, the presence of calves and their age may be an influencing factor on fewer observations of resting groups during summer[103], since the peak calving month in this area is July[103] (JC, unpublished data) and common dolphin calves are known to be most vulnerable during the first three months after birth[114–116]. Considering party size and spatial cohesion of common dolphin groups that were investigated in the study of Castro et al. (2022), and data on party composition of the same species derived from other studies around the world[117], the social dynamics of common dolphins in South Portugal are suggested to correspond to the most fluid category of the fission-fusion dynamics framework proposed by Aureli et al. (2008)[25].

Common dolphins (*Delphinus spp.*) are known to occur in pods of tens to hundreds or, in some cases even thousands of individuals and represent a highly social and gregarious dolphin species[118]. An early study from Amos (1999) suggested a matrilineal social structure for the species[16], whereas more recent studies indicated a social system characterized by fission-fusion dynamics[40,48] which is further supported by findings of relative large testis size suggesting strong sperm competition within the species[19]. A recent study from Ball et al. (2017) investigated the relatedness of common dolphin (*D. delphis*) individuals of pods sampled along different locations along the Portuguese coast using microsatellite analysis[38]. They found, that groups of the species occurring in this region did not consist of closely related individuals, which is a contrasting result to the kinship related social systems in other delphinids such as killer whales and pilot whales[54,119]. However, kinship analysis of common dolphin groups revealed a certain extent of natal philopatry whereby most groups that contained kin were found in the same or neighboring geographic location, which is a similar finding to the fission-fusion structures of bottlenose dolphins[40,120]. Further, the results of the study indicated higher kinship between males than females, with female kin individuals dispersing geographically further than male individuals[38]. Hence, the authors suggested a female-biased dispersal of *D. delphis* in the Northeast Atlantic. There are several hypotheses to explain such gender-based social structures. One potential driving mechanism may be the avoidance of inbreeding events, leading to low associations between offspring and parents[38]. Additionally, field observations during the study of Ball et al. (2017) are consistent with findings that male common dolphins have a relatively large testis size that may result in high reproductive competition between males, ultimately setting females under enormous stress[19,121]. Thus, female dispersal from groups over large geographical distances might be a response in order to avoid male harassment[38]. Juvenile and female common dolphins are known to show feeding strategies different from adult male individuals[96,122]. Due to their smaller size, female and juvenile individuals are thought to have a disadvantage in competing for food resources within a group containing adult males[123,124].

Female-biased dispersal patterns in common dolphins may therefore be a mechanism to avoid high food competition with adult males[38].

Another study focused on a common dolphin (*D. delphis*) population in the semi-enclosed bay of Port Philip in Southeast Australia. Dolphin groups were shown to form cohesive social structures, while some individuals seemed to have preferred conspecifics to associate moderate to strong bonds with[41]. In the study area, the resident 30 individuals exhibit a high degree of site fidelity and residency throughout the year, though it has to be noted that most of the individuals were resident females with calves[125]. The authors suggest, that one of the reasons why the community in Port Philip consists of only 30 individuals, may be that the embayment has reached its carrying capacity for the species with regards to prey availability[41]. Mason et al. (2021) identified strong bonds between five adult dolphin pairs, with six adult pairs being preferred companions[41]. Other associations were characterized by short-term casual acquaintances underlying rapid association and dissociation patterns[41]. Out of twelve adults, seven individuals showed a more gregarious behavior than the average while the central individual, the only confirmed male, was found to be the most gregarious individual[41]. Contrasting to common dolphins around the world that are mainly observed to be a gregarious species characterized by highly fluid fission-fusion dynamics[40], the population in Port Philip shows extraordinary stable social bonds[41]. In shelf and gulf waters off South Australia, common dolphin pods usually consist of equal gender ratios[48,126]. However, the majority of common dolphins found in Port Philip were females with their offspring, suggesting that the area may function as a nursery ground[125]. Possible driving factor for the unusual high cohesion and strong social bonds of common dolphins in Port Philip in contrast to their offshore conspecifics that exhibit highly fluid fission-fusion dynamics, may be the restriction to a small geographic space due to the embayment and the relatively stable and predictable availability of food resources within the area that creates favorable conditions for stable groups of individuals[41]. Further, the embayment is thought to facilitate a natural protection from predators due to its narrow entrance and sheltered waters which in return enhances the areas' function as nursery ground for females with calves[125].

1.3 The use of unmanned aerial vehicles for wildlife research

Unmanned aerial vehicles (UAVs), commonly known as "drones", are a rather novel technology and experienced a rapid development over the past years, attracting not only individuals but also governments and science[127]. Generally, UAVs may be distinguished between two types: 1) Fixed-wing (FW) UAVs and 2) Vertical take-off and landing (VTOL) UAVs (*Figure 1.2*).

Figure 1.2: Fixed-Wing and Vertical Take-Off and Landing UAV

Fixed-wing systems are usually larger in size, with a wingspan of up to 3 m, and in shape and function comparable to airplanes, therefore requiring a runway for launch and landing. Due to integrated autopilot capabilities, these systems require little control from the pilot once aloft. FWs are able to reach much higher altitudes, velocities and distances from the launching point compared to VTOLs, making them ideal for the use in remote locations that would be unsafe or inaccessible for observers aboard manned aircrafts or VTOLs[128,129]. Their capabilities make them suitable for a variety of applications except such including research that requires fixed positions, low altitudes or slow movements as needed in behavioral studies[130].

The functionality of VTOL systems is comparable to the dynamics of helicopters. Most models use 4 – 8 rotors that enable the aircraft to hover in a stationary position, stay in low altitudes, move slowly and allow for vertical take-offs and landings thus eliminating the need for a runway. Additionally, commercial models include built-in high-definition cameras with mechanical image stabilizers (i.e., Gimbal), allowing the pilot to capture videos and/or pictures in high quality from an advantageous perspective. Further, VTOLs are generally lightweight (< 5 kg), portable, cost-effective and readily available from several commercial manufacturers. However, such systems require active controlling by a remote pilot and their maximum flight distance is limited to a range of tens of kilometers, while the battery life of around 30 – 45 min only allows for rather short air-times in smaller survey areas compared to FWs.

The advanced properties of modern VTOL UAVs make them suitable for various wildlife-related applications, becoming an increasingly popular and useful tool in natural sciences. They are used for a variety of wildlife-related applications including behavioral studies, population assessments[131], the collection of biological samples[132], research on large terrestrial mammals[133–136], monitoring of birds[137,138], primates, reptiles, wildlife habitat assessment and modeling as well as wildlife conflict management[139] and marine mammals[129,131,140–142]. Their success in this field may be explained by the diversity of existing

UAV models and their countless ways in which they can be operated[139], while still being cost-effective and viable systems that produce systematic data of high temporal and spatial resolution[143].

A comparative study of sampling precision of nearshore marine wildlife between manned and unmanned aerial surveys revealed numerous advantages of UAVs in this field: i) Post-hoc video analysis of UAV footage provided more precise and accurate estimates of observed marine mammals while they were less likely to miss animals within the study area[144], ii) video analysis were more reliable particularly for dolphins due to the capability of replaying important sections of the footage allowing for more accuracy and reducing the chance of misidentification[144] and iii) the capability of replaying footage reduced the need of multiple observers in order to minimize bias, as needed for manned aerial surveys[145,146]. Further, fatigue of observers that spend hours monitoring animals in large areas while dealing with high levels of noise is eliminated in unmanned surveys, because footage may be stopped and replayed at any time which in return increases survey accuracy[131,147].

Despite the numerous advantages of the use of unmanned aerial vehicles for wildlife research, the technology has limitations and little is known about the impacts that UAVs may cause on wild animals[148–150]. Different populations in the wild might show idiosyncratic responses to the presence of an UAV depending on various factors such as species, life history stage, habitat, environmental conditions (e.g., weather, water clarity, waves) or type of UAV and the method of operation (e.g., noise emitted, velocity, distance) which may affect the perception of risk in wild animals[142,151,152]. Considering small cetacean species (e.g., delphinids), behavioral responses as reaction to an approaching UAV remains scarcely investigated[153]. However, current evidence indicates that UAVs flying at low altitudes (< 30 m above sea-level) nearby bottlenose dolphins (*Tursiops truncatus*) trigger short-term behavioral responses of the species[130,154,155]. Fettermann et al. (2019) found, that the number of reorientation and tail slap events of *T. truncatus* in New Zealand (near Great Barrier Island) increased when flown at 10 m altitude, whereas there was no significant difference in dolphin behavior when flown at 25 m or 40 m, respectively[156]. A study of Castro et al. (2021) revealed, that short-beaked common dolphins (*Delphinus delphis*) in the south of Portugal performed significantly more direction changes when the UAV was operated at 5 m altitude compared to higher altitudes[140]. Considering the growing findings of how UAVs may disturb and alter wildlife behavior, it is crucial to investigate and understand the impacts of unmanned aerial vehicles on the studied species in order to accurately interpret any data collected by such a system.

Manned aerial vehicles such as helicopters or light aircrafts have originally been used to conduct aerial surveys and in fact, still remain the best option for monitoring projects in large areas[157]. Such surveys require the availability of appropriate aircraft and fuel in the study region in addition to a trained pilot, making them cost-intensive and particularly difficult in developing countries[143]. Moreover, aircraft crashes are known to be the greatest cause of death for biologists[158] making aerial surveys with manned aircrafts highly risky operations[159,160]. Furthermore, manned aircrafts are likely to bring forth bias in behavioral studies, as they exhibit high auditory and visual impacts for observed wildlife[161,162]. However, considering costs and benefits manned aircrafts would currently be more efficient than UAVs for marine surveys over large areas, mainly due to restrictions regarding the maximum flight distance of UAVs[163]. On the other hand, when intensive sampling of smaller areas (< 10 km^2) is required, UAVs were found to be the better option[144,163].

1.4 References of the general introduction

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Behavior and fission-fusion dynamics of common dolphin (*Delphinus delphis*) groups with calves in the South of Portugal

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2. Manuscript

2.1 Abstract

Fission-fusion dynamics describe animal social systems that are fluid and characterized by varying group sizes. Costs and benefits associated with grouping are considered to be the driving force for separation (fission) and joining (fusion) of individuals, resulting from ecological (e.g., food availability, predator abundance) and social (e.g., behavioral state, presence of calves) factors. The behavioral state gives insights into an animal's ecology, and allows to better protect the species or population by understanding their strengths and vulnerabilities. The present study investigates which factors influence behavioral state and fission-fusion dynamics in common dolphin (*Delphinus delphis*) groups with calves in the south of Portugal. Between June and October of 2016, 2017 and 2019, 39 UAV-based focal follows were conducted, resulting in 768, 30-second behavioral samples (384 minutes). A multinomial model based on generalized estimating equations framework was used to model: i) the behavioral state by testing the responses to group size, total number of calves and month; ii) and fission-fusion dynamics assessing the effect of behavioral state, month, total number of calves and time of the day. The behavioral state of dolphin groups with calves was statistically significantly affected by the total number of calves and month. As the number of calves increased, *resting* behavior was less likely to occur than *travelling* (OR = 0.7, p = 0.015). Dolphin groups with calves were less likely to be *socializing* in *July* than to *travel* in *June* (OR = 0.1, p = 0.021). Group size had no statistically significant influence on the behavioral state in the present study. This study also revealed, that common dolphins in the south of Portugal exhibit a high rate of fission-fusion dynamics, but were not influenced by the factors considered in this study (i.e., behavioral state, month, total number of calves and time of the day). By assessing behavior and fine-scale social dynamics in common dolphins, this study enhances the current understanding of ecological and social aspects shaping grouping patterns and behavior in common dolphin groups with calves. This study also highlights the advantages of using unmanned aerial vehicles (UAVs) to assess behavioral data in wild animals.

Keywords: Behavior · Cetacean · Calves · Social structure · Grouping patterns · Unmanned aerial vehicles

2.2 Introduction

Sociality is a widespread behavior in mammals and possibly evolved when the benefits of associations between individuals exceeds the costs[1]. Association patterns of individuals may respond to several social (e.g., behavioral state, kinship, gender, mating) and ecological (e.g., food availability, predator abundance) factors to maximize benefits (e.g., increased access to food and mates, decreased predation risk) and minimize costs (e.g., competition for food) of grouping[2,3]. Ultimately, the tradeoffs between these factors have an impact on the social structure of species and/or populations, and survival of individuals and offspring[3–6].

The extent of variation in individual membership and the spatial cohesion of a group over time may be referred to as "fission-fusion dynamics" (hereafter: FF-dynamics)[7]. "Fission-fusion" describes the joining (fusion) and leaving (fission) of individuals to or from a group. Any animal society may be characterized by its degree of FF-dynamics ranging from highly fluid (flexible membership) to highly cohesive (stable membership)[7]. Aureli et al. (2008) proposed three dimensions of FF-dynamics: 1) the temporal variation in spatial cohesion among group members, 2) the temporal variation in group size and 3) the temporal variation in group composition. The classification of a species or population within a multidimensional FF-model, allows to investigate qualitative and quantitative differences of the species/population fission-fusion social system[7]. Since dolphin species exhibit a high degree of intra- and interspecific variation in group size[8], they are an appropriate taxon to investigate variables and responses within FF-dynamics.

Within the marine mammals, dolphins represent the most widespread and diverse of all cetacean families[9], and are characterized by large variations in social structures[10]. For example, killer whales (*Orcinus orca*) are known to live in stable, primarily matrilineal groups[11–13] whereas Hector's dolphins (*Cephalorhynchus hectori* – Bräger 1999) live in highly fluid social systems[14]. Dolphin species may exhibit intra-specific variations in their social structures[8]. Short-beaked common dolphins (*Delphinus delphis*) in the south of Portugal were found to exhibit highly fluid social dynamics,[15] whereas Amos (1999) suggested a matrilineal social structure for the species[16]. Behavioral state has impacts on fission-fusion dynamics, for instance, Indo-Pacific humpback dolphins (*Sousa chinensis*) in Cleveland Bay, Australia, were found to exhibit variable group sizes ranging from one to 12 animals[17]. In general, school sizes were significantly larger when socializing than travelling or foraging[17]. In Sarasota Bay, USA, bottlenose dolphins form large groups when resting to minimize predation risk while building small foraging-groups to decrease feeding competition[18].

The presence of females and/or mother-calf pairs can be also an important factor for grouping patterns. Ball et al. (2017) found, that groups of *D. delphis* along the coast of Portugal are underlying female-biased dispersal, possibly as a response to local ecological factors specific to the studied population[19]. Juvenile and female common dolphins are thought to have a disadvantage when foraging alongside adult males, due to their smaller size and different feeding strategies[20,21]. Thus, the authors suggested female-biased dispersal as a mechanism to avoid food competition with adult males[19]. Although common dolphins are generally characterized by highly fluid social systems[22], a population in Port Philip, Australia, exhibited extraordinary stable bonds and site-fidelity[23]. The majority of common dolphins in the embayment were females with their offspring, indicating that the area may function as nursery ground for the species[24]. Nursery groups may decrease predation[8] and infanticide[25,26] risk while minimizing feeding competition of mothers and calves whose foraging strategies differ from those of the larger adult males[27,28]. A study in the south coast of Portugal revealed as well, that the presence of mother-calf pairs affects the group size of common dolphins[15]. Groups were more stable, less social and larger when at least one mother-calf pair was present[15]. Larger groups provided enhanced predator protection considering the dilution effect, being beneficial for the survival of females and offspring[29–31].

In addition to behavioral state and presence of mother-calf pairs, seasonality may also influence the social dynamics and behavioral state of delphinids. Common dolphins in the Algarve region, Portugal, were more likely to forage (than travel) in June than in September and October, which is likely to be linked with seasonal changes of prey availability[32]. In contrast, resting behavior was more likely to be observed during the month of September compared to June[15], which is suggested to be linked with seasonal changes of predator abundance[29] and anthropogenic pressure from tourism peaks during summer[33]. Further, the daytime seems be another important factor influencing fission-fusion dynamics. The odds of fusion events after midday (12 am) were significantly lower compared to the morning period (9:00 – 11:59 am) and stable groups[15].

In the south coast of Portugal, the common dolphin (*Delphinus delphis*) is the most abundant cetacean species[34,35] and yet, little is known about its ecology and biology in this area[36]. The species feeds on a variety of pelagic schooling fish off the coast, but preferably on *Sardina pilchardus*[37–39]. Within the region, killer whales[40] and several shark species[41–43] (e.g., hammerhead sharks, blue sharks etc.) are potential predators for common dolphins.

Unmanned aerial vehicles (UAVs), commonly known as “drones”, are a rather novel technology and experienced a rapid development over the past years, attracting not only individuals but also governments and science[44]. The advanced properties of modern VTOL (vertical take-off and landing) UAVs make them suitable for various wildlife-related applications, becoming an increasingly popular and useful tool in natural sciences. They are used for a variety of wildlife-related applications including behavioral studies, population assessments[45], the collection of biological samples[46], research on large terrestrial mammals[47–50], monitoring of birds[51,52] and marine mammals[45,53–56]. Their success in this field may be explained by the diversity of existing UAV models and their countless ways in which they can be operated[57], while being cost-effective and viable systems that produce systematic data of high temporal and spatial resolution[58]. The capabilities of VTOL UAVs for wildlife research (e.g., privileged view on the studied species), make them an appropriate tool to investigate fission-fusion dynamics of small delphinid species.

Castro et al. (2022) revealed that *D. delphis* inhabiting the southern coast of Portugal has a highly fluid social system with month, daytime and presence/absence of calves significantly impacting fission-fusion dynamics of the species. Therefore, a directed study focusing on groups with calves may give additional insights into social dynamics of common dolphins. In this study, I investigated the potential influence of month, group size and number of calves on the behavioral state of groups with calves and month, behavioral state, number of calves and sampling hour on the fission-fusion rate of dolphin groups with calves.

2.3 Materials and Methods

2.3.1 Study site and aerial surveys

Two different multirotor vertical take-off and landing (VTOL) UAVs (DJI Phantom 2 and 4; 35 cm diameter, 1 kg and 1.38 kg respectively, plastic propellers, http://www.dji.com) were used with an attached GoPro HERO4 camera in combination with a radio antenna system to enable video live-streaming during flights. The study site was located in the south coast of Portugal (Algarve region), between Olhão (37°1.56´N, 7°50.54´W) and Cape St. Vicente (37°1.35´N, 8°59.81´W) at a maximum distance from shore of 25 nautical miles (nm) (*Figure 2.1*). All data sampling and observations during the study period were conducted under the authorization of the Portuguese Conservation Institute (ICNF-AOC/17/2016).

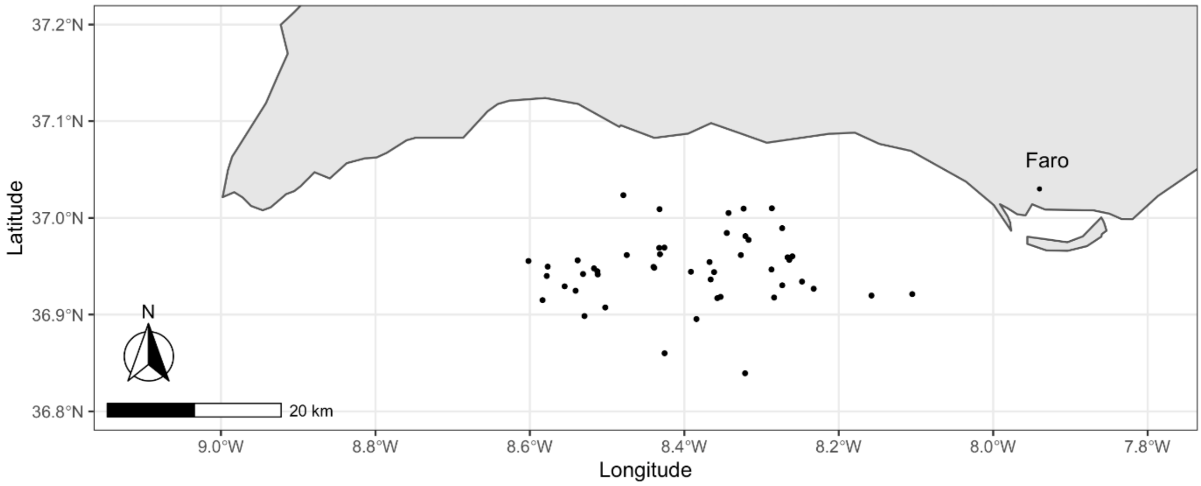

Figure 2.1: Starting points of all conducted UAV flights

Random surveys were conducted during the spring, summer and autumn months (June-October) of 2016, 2017 (DJI Phantom) and 2019 (DJI Mavic 2 Pro) in order to locate common dolphin groups. Surveys were carried out from a research vessel (7 m RHIB, 4-stroke 135 hp outboard engine) at an average speed of 12 knots with good visibility (> 5 km), swells of < 1.5 m, sea state conditions of Beaufort 0 – 3 and no precipitation. The GPS positions of common dolphins were recorded with a Garmin echoMAP™ 42dv. Only groups with confirmed calves or newborns (individuals with ≤ ½ the length of an adult, travelling alongside an adult; Castro et al. 2020)[36] were sampled. The sampling technique adapted was the focal follow[59], consisting of following a single group and for posterior recording of social interactions and group characteristics (e.g., group size, number of calves) in regular periods of time (i.e., "beep" – definition in the section Video Analysis). The UAV was launched and retrieved manually from the vessel with a downwind orientation and the engine in neutral. Once the UAV was aloft, the research vessel maintained a distance of 30 – 100 m from the group to minimize impacts of the vessel on the dolphin's behavior. Sampling was only conducted when no other boats were present within a 1 nm radius. These sampling criteria were intended to ensure suitable conditions for observations and accurately determining changes in tested variables while controlling the effect of environmental conditions.

During the surveys, a boat driver, UAV pilot and dolphin observer(s) were present on the research vessel. After launching the UAV, it was flown towards the dolphin group to start the focal follow. A focal follow ended, if the group was lost for 2 minutes in a row, if the calves left the frame for 2 minutes in a row, if visibility was impaired (e.g., due to sunglare or height of the UAV) or the UAV battery reached 30% remaining capacity (flight duration with a fully charged battery limited to 25 min). The flight height was chosen balancing two aspects:

guarantee the capture of the entire group in the screen as best as possible; and maintaining a minimum height of 20 m to minimize possible impacts of the UAV on the animals' behavior (see details in Castro et al. 2021)[54]. To avoid group resampling between focal follows, each new focal follow took place after travelling at least 1 nm and/or 1 hour in the opposite direction of the group previously sampled. The behavioral data and group characteristics were collected based on the video footages.

2.3.2 Video analysis

Videos from both UAVs were analyzed visually using VLC media player (64 Bit; Version: 3.0.17.4 – from April 19, 2022). A dolphin "Group" was defined following the 10 m chain rule and by the level of coordinated activity of individuals[60–62]. According to Wells et al. (1987)[63], the maximum distance between two individuals belonging to the same group was considered to be 100 m.

During video analysis, the entire group was systematically scanned and focal follow data were collected in sampling intervals of 30 seconds – "beep"[59,64], namely: the group size, number of newborns/calves and dominant behavioral state of the group. Four different behavioral states were recorded: *foraging*, *resting*, *socializing* and *resting* (*Table 2.1*). When multiple behaviors were observed, the "dominant" behavior (i.e., when > 50 % of individuals exhibited the same behavior) was recorded. The data collected for each variable was done by the same observer.

Table 2.1: Definition of behavioral states considered in this study and based on Pearson (2009) and Castro et al. (2021)

Behavioral State	Definitions
Foraging	Act of feeding on prey or looking for it: Characterized by long, deep dives followed by strong blows; May involve rapid coordinated "burst swims", noiseless headfirst re-entry leaps, coordinated clean leaps and tail slaps
Resting	Slow movements with no apparent direction; Shallow dives and low activity; sometimes floating/drifting at or near the surface
Socializing	Diverse interactive moments with each other or inanimate objects; No apparent direction; May involve body contact and pectoral fin rubbing; behaviors such as rolling, belly-up swimming, spyhops, splashing near surface, chasing, leaping, mating and playing with seaweed are included
Travelling	Moving steadily coordinated in one direction

2.3.3 Statistical analysis

Objective 1: behavioral state

The potential effect of months, group size and number of calves on the behavioral state was analyzed. Considering the limited number of observations for *foraging* (n = 2) this class was excluded from the statistical analysis for both objectives (i.e., behavioral state and fission-fusion dynamics). To relax the independence assumption, a generalized estimating equation (GEE)[65] approach was used that allow to account for temporal proximity between observations (beeps) within the same focal follow. To model behavioral state, a multinomial framework appropriate for multi-level responses was adopted[66], fitted assuming a baseline category logit model for the marginal probabilities and using an exchangeable correlation structure. This correlation structure is recommended for nominal responses[65,66], and does not assume time dependency between observations. A forward model selection procedure was implemented to examine the performance of additional candidate variables. This procedure was implemented using Wald test.

In multinomial models, a baseline category for each variable considered is defined and the model results are expressed as joint outputs. For behavioral state, *travelling* was defined as the baseline category of the response variable, while *June* was defined as baseline for month, and for group size and total number of calves in the group (both coded as continuous variables) the baseline category was defined as zero. The regression coefficients of the multinomial GEEs can be expressed as odds ratio (OR), which compare the likelihood of a baseline with the likelihood of occurrence of other pairs of categories. Odds ratio can vary between (i) OR = 1 indicating equal likelihood between pairs under comparison, (ii) OR > 1 which indicates that the occurrence of one event is associated with higher odds of the other, and (iii) OR < 1 indicates the presence of one event decreased the odds of others[67].

All statistic procedures were done using R version 3.6.0[68], with RStudio v. 1.3.1056[69]. Multinomial-GEEs were fitted using nomLORgee and Wald test was calculated using waldts function, both from the multgee package[65]. Collinearity among variables was from the performance package[70] and model coefficients were displayed using ggplot2 package[71], while regression Tables were formatted using sjPlot package[72].

Objective 2: fission-fusion dynamics

An equivalent modelling approach was followed for the fission-fusion dynamics, but using months, number of calves, behavioral state and sampling hour as predictors. For the response variable, the level *stable* was defined as baseline while for the predictors *June* was defined as baseline for month, *travelling* for the behavioral state, *zero* for the total number of calves and *10 am* for sampling hour.

2.4 Results

I conducted 39 focal-follows, resulting in ~ 18 hours of video footage of which ~ 6 ½ hours (384 minutes) were used for analysis. The largest group consisted of 69 individuals (*Figure 2.2*), and the average group size was 22 (± 15) individuals, but most observations were of groups with less than 40 individuals. The maximum number of calves within a group were 12 individuals (*Figure 2.2*), and there were 4 (± 3) calves in a group on average. It is important to note, that many values for group size and the total number of calves correspond to observations of the same group in different time periods. The greatest change in group size between two beeps was 41 individuals (82 %), whereas the in percentage the greatest change was 1150 % (i.e., from 2 to 23).

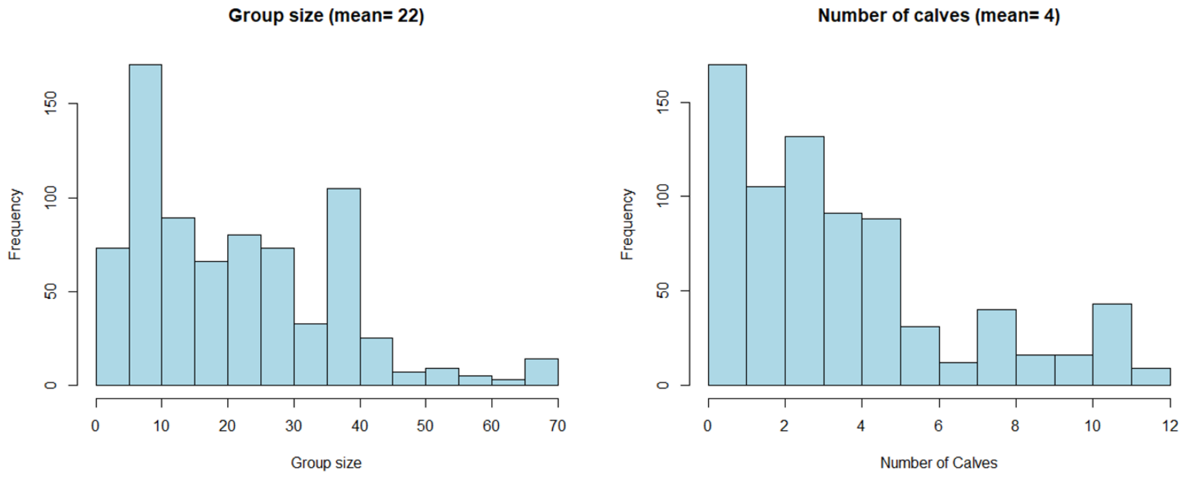

Figure 2.2: Frequencies of *group size* and *number of calves*

The most observed behavioral state was *travelling* corresponding to 89 % of the 30 second interval records, followed by *socializing*, *resting* and *foraging* (*Figure 2.3*). Overall, there were 16 cases in which behavioral state could not be determined. The main structure of groups remained stable (55 %), while fission and fusion events were equally frequent observations in this study (*Figure 2.4*).

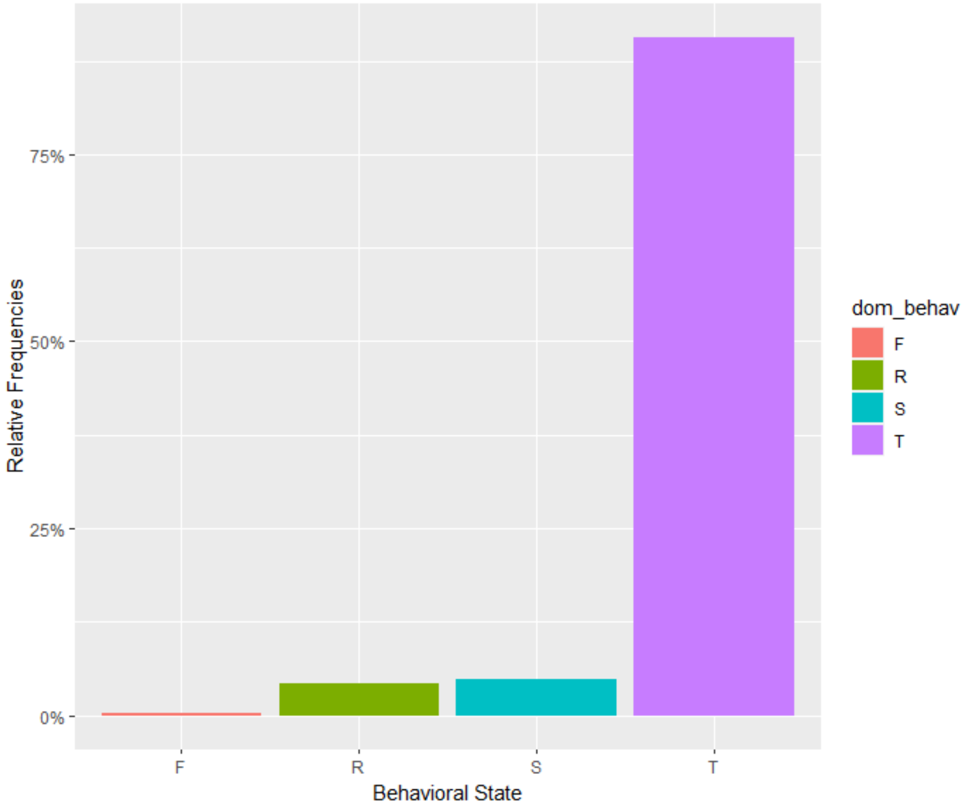

Figure 2.3: Relative frequencies of observed behavioral states. *Foraging* (F), *resting* (R), *socializing* (S) and *travelling* (T)

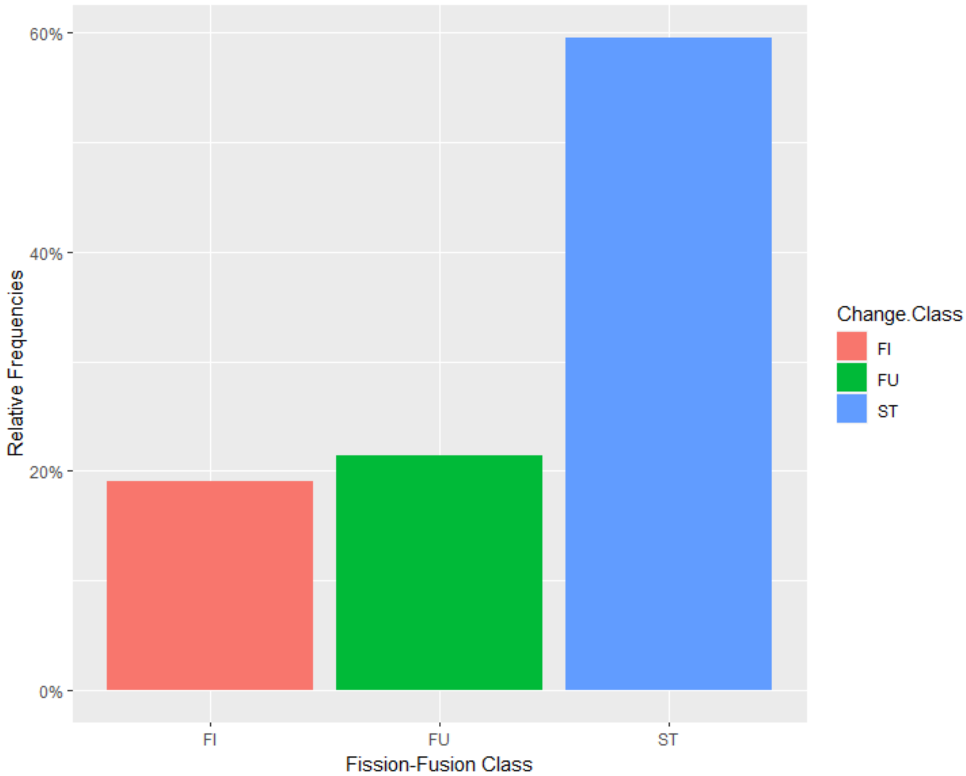

Figure 2.4: Relative frequencies of observed fission-fusion classes. *fission* (FI), *fusion* (FU), *stable* (ST)

2.4.1 Behavioral state (objective 1)

According to Wald's test, two potential variables were identified with a significant effect on the behavioral state, namely: the month and the total number of calves. A final model using these two variables as predictors was tested, however it failed due to convergence issues possibly because of large differences between the number of observations in each behavioral class (*Figure 2.3*). Therefore, the effect of the two variables was assessed independently (*Table 2.2*). For month, the model identified significant differences when comparing *socializing* in *July* with *travelling* and *June* (i.e., the baseline) (OR = 0.1, p = 0.021) (*Figure 2.5*). The odds ratio in this case is near to zero, meaning that *social* behavior in *July* is less likely than the baseline. There were no observations recorded in *July* for *resting*, and therefore the model estimated possible large differences (OR = 0, *Figure 2.5*). The model testing the effect of the group size did not perform better than the null model (*Table 2.2*).

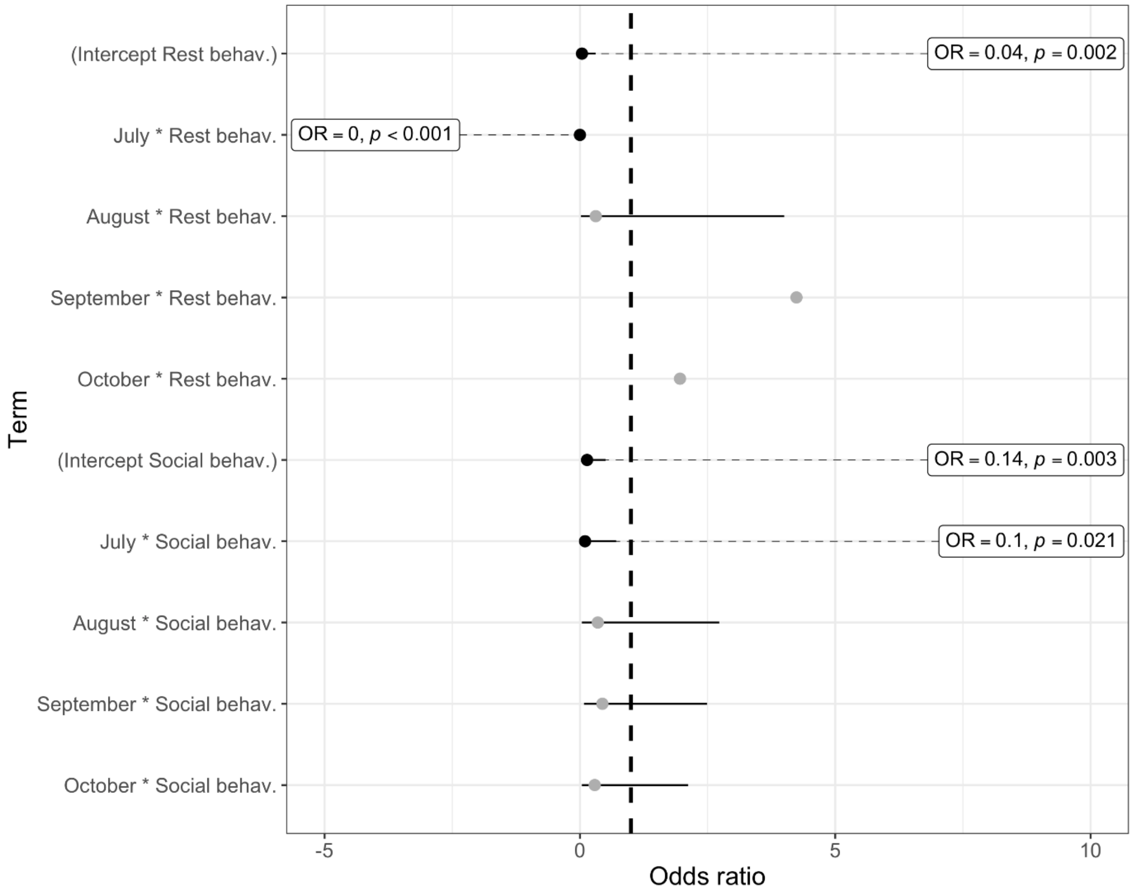

Figure 2.5: Plot with estimated odds ratios (dots) of the marginal model and respective confidence interval (whiskers) from the model for the behavioral state using months as predictor. The baseline is *June* for month and *travelling* for behavior. Significant results (i.e., p < 0.05) highlighted by the black dots.

Table 2.2: Goodness of fit based on the Wald test for the models for behavioral state. The model formula is structured as "response variable~covariates", with the operator ~ meaning "as a function of". DF (degrees of freedom)

Candidate models			
M0: *Behavioral State ~ 1 (null model)*			
M1: *Behavioral State ~ Month*			
M2: *Behavioral State ~ Group size*			
M3: *Behavioral State ~ Number of calves*			
Model comparison	**Wald statistics**	**DF**	***p***
M0 *vs.* M1	2509.78	8	<0.0001
M0 *vs* . M2	34.422	2	0.1789
M0 *vs* . M3	127.632	2	0.0017

When comparing the *number of calves* during *resting* with the *number of calves* when *travelling*, the results were statistically significant (p = 0.015) (*Figure 2.6*). The odds ratio (OR = 0.7) indicated that it was less likely to have higher numbers of calves during *resting* than in groups that are *travelling*. In fact, the highest number of calves observed in *resting* groups was 4 individuals, whereas *travelling* occurred with as many as 12 calves.

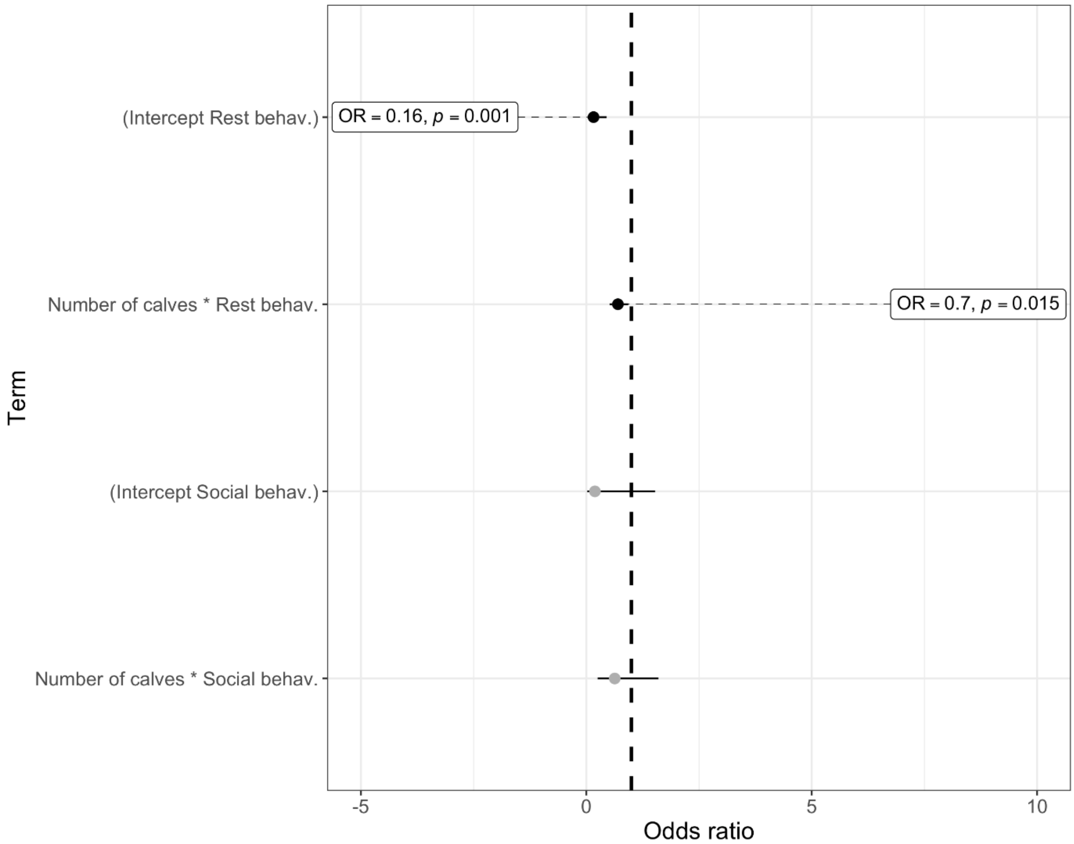

Figure 2.6: Plot with estimated odds ratios of the marginal model (dots) and respective confidence interval whiskers from the model for behavioral state vs. number of calves. The baseline is *0* for number of calves and *travelling* for behavior.

2.4.2 Fission-fusion dynamics (objective 2)

From all potential predictors tested to model FF-dynamics, no models performed better than the null model except the model fitted with *month* ($p < 0.0001$, *Table 2.3*), meaning that including this variable as predictor had a positive effect on the fitting of the model. However, the model output using month as predictor showed that none of the levels of *month* had significant influences on fission-fusion rate. When modelling with *behavioral state* as predictor, the model failed, so that its' influence on the fission-fusion rate couldn't be analyzed. This result suggests that none of the selected predictors (i.e., *month*, *number of calves*, *hour*) had a significant impact on the fission-fusion rate of common dolphin groups in the present study.

Table 2.3: Goodness of fit based on the Wald test for the models for fission-fusion rate. The model formula is structured as "response variable~covariates", with the operator ~ meaning "as a function of". DF (degrees of freedom)

Candidate models
M0: *Fission-fusion rate ~ 1 (null model)*
M1: *Fission-fusion rate ~ Month*
M2: *Fission-fusion rate ~ Number of calves*
M3: *Fission-fusion rate ~ Hour*

Model comparison	Wald statistics	DF	*p*
M0 *vs* . M1	114.437	8	<0.0001
M0 *vs.* M2	32.459	2	0.1973
M0 *vs.* M3	14.721	2	0.479

2.5 Discussion

In this study, the average group size of common dolphins was 22 (± 15) animals, which is between that reported by two previous studies in the studied area (average = 15; Castro et al. 2022 and average = 31; Castro et al. 2020). This value is within the most frequently observed group size for common dolphins in the North Atlantic (20 – 30 animals; Evans 1994), and in New Zealand (21-30 animals; Stockin et al. 2008). The differences observed in the average group size with the findings of Castro et al. (2020, 2022) may be due to different sampling methods. The use of UAVs for sampling provided an advantageous vertical view on the groups allowing to count animals on the screen, repeatedly if necessary. Castro et al. (2020, 2022) did not have this advantage, since sampling was done visually from the research vessel. Counting animals visually from a vessel can have limitations: submerged animals can't be seen, animals may be hidden behind waves or whitecaps, and animal behavior can make it difficult to assess the actual numbers of individuals. On the other hand, counting animals from frames of a UAV video does not have those limitations, or only in reduced levels. From a vertical perspective, submerged animals can still be seen[73] and diving or highly active animals can be tracked much easier, further simplified by the capability to stop and replay difficult sections of the video. Nevertheless, battery capacity, sunglare and precipitation represent limitations of the method, as well as the risk of losing the UAV. Counting animals from a video may be more accurate than counting on the field from a vessel. Fettermann et al. (2022) found, that UAV-based abundancy counts detected 26.4 % more individuals per group than boat-based counts on average.[73]

This study revealed, that the number of calves had a significant influence on the behavioral state of common dolphin groups in the south of Portugal. Higher numbers of calves were less likely to occur in *resting* groups than in those *travelling*. This is partly consistent with a previous study on the species in the same region[15]. The authors found, that the presence of mother-calf pairs significantly influenced dolphin behavior[15]. The present study enhances the current understanding, by revealing that not only the presence, but also the number of calves in a group has significant influences on the group's behavioral state. *Resting* may occur with fewer calves than *travelling*, because lower numbers of calves may be easier to protect and supervise than higher numbers. During *travelling*, the whole group has a higher activity level compared with *resting*, likely making it more difficult for potential predators to approach the group. In return, this may allow more calves to be present in *travelling* groups without taking unbearable risks. Further, a recent study has revealed that overall group size of common dolphins in the south of Portugal decreased during *resting*[15]. Hence, when overall group size of *resting* (vs. *travelling*) animals is generally lower, it is more likely to have fewer calves within the group. The implementation of both, group size and total number of calves as covariates for the response variable 'behavioral state' into a GEE modelling process failed, most likely because of the too small sample size. Hence, more sampling would be required to investigate if *resting* with low numbers of calves occurs due to generally smaller *resting* groups or for other reasons. Future studies should increase the sampling effort in order to maximize observations of all behavioral states of interest.

Comparing the behavioral state over months showed that *travelling* in *June* was more likely than *resting* behavior in *July* ($p < 0.001$). Consistent with Castro et al. (2022), one could imply that common dolphin groups with calves may be driven by maternal vigilance at the expense of resting[74,75], since the peak calving month in the study area is July (JC, unpublished data)[15]. However, as previously mentioned the odds ratio (OR = 0) for this case implies, that it was completely unlikely for *resting* to occur in *July*. In fact, no observations for resting were recorded in the video footages made in *July* and therefore, this result is unlikely and probably occurred due to sampling issues. The analysis of the two-ways table for behavioral state vs. month revealed, that there were zero observations (n = 0) for groups exhibiting *resting* behavior during the month of *July*, explaining not only the unusual odds ratio but also the high level of significance. In this case, the findings do not result from ecological reasons but rather from a lack of observations for the tested behavioral states. Hence, the sampling effort needs to be increased in future studies in order to obtain ecologically interpretable results.

It was less likely for groups to *socialize* (vs. *travel*) in *July* compared to *June*. Again, the calving season in the study area may also contribute to explain this result. Castro et al. (2022) have shown, that mother-calf pairs in the area are less likely to occur in groups that are socializing[15], possibly to reduce male harassment by separating from groups that exhibit mating behavior[8,76–78]. Assuming that the peak calving month is *July* and considering that only groups with calves were sampled, it may be possible that during and after *July* mother-calf pairs started separating from groups displaying social behavior, resulting in lower odds for *socializing* groups with calves in this month. Further, if *July* would be the peak calving month, then there would be less newborns in *June*. Less newborns mean that fewer numbers of mother-calf pairs would segregate from *socializing* groups during *June* compared to *July*. However, for *socializing* groups in *July* there were only seven observations overall, while there were 127 observations of *travelling* in *June*. The discrepancy of observations rather than ecological reasons may have led to the significant findings. Increasing the sample size may help to confirm or refute this result.

In the present study, *foraging* was observed only two (n = 2) times in total. Because of the insufficient number of observations, this behavioral state has been excluded from the models. However, Castro et al. (2022) found that dolphins were less likely to forage (vs. travel) in autumn (September and October) than in summer (June)[15]. The authors explained these findings through prey behavior (e.g., spawning), availability and distribution[79–81] and primary productivity[82,83], which peaks during spring/summer. Primary production peaks are likely to cause increased prey abundance[32,84], which in return favor foraging behavior of dolphins. A reason for the differences in observation numbers for *foraging* between the present study and the study conducted by Castro et al. (2022), may be the different sampling strategy (i.e., UAV) that was used. Fettermann et al. (2022) found, that UAV-based surveys recorded *foraging* in bottlenose dolphins (*Tursiops truncatus*) 58.3 % less frequently compared to boat-based surveys.[73] Further, it may be possible that common dolphins avoided to feed when the UAV was in proximity, as it has been revealed that UAVs may impact dolphin behavior.[54,85] However, literature on the impact of UAVs on dolphin behavior is scarce, and it is unlikely that only *foraging* would be impacted. Future studies should increase the sampling effort in order to cover the behavioral patterns properly. Although some literature on the impact of UAVs on cetacean behavior is already published[54,85,86], more studies focusing on the behavioral impact of UAVs on dolphin species would enhance the knowledge on dolphin behavior allowing for better interpretations of behavioral data collected by UAVs.

In the present study, the fission-fusion rate of common dolphin groups with calves (37 %) was approximately 2.2 times higher than for Guiana dolphins (17%)[87] and about 12 % higher than observed for the same species in the same study area (33 %)[15]. Guiana dolphins are considered to exhibit a high degree of fission-fusion dynamics[87], and a recent study from Castro et al. (2022) in the south of Portugal related common dolphins with the most fluid category of the framework for fission-fusion dynamics proposed by Aureli et al. (2008)[7,15]. The observed rate in the present study supports and consolidates the suggestion, that common dolphins in the south of Portugal exhibit a high degree of fission-fusion dynamics and may correspond to the most fluid category of the framework. Castro et al. (2022) revealed, that the presence of mother-calf pairs is the primary factor influencing fission-fusion dynamics of common dolphins in the south of Portugal. This finding may explain, why none of the predictor variables tested (i.e., behavioral state, month, hour and total number of calves) in the present study affected FF-rates, because only common dolphin groups with calves (i.e., the predominant influence on FF-dynamics)[15] were considered. Since fission-fusion events at the level of the individual were not recorded in the present study, it is possible that fission-fusion events happened during a sampling interval, but because group size remained the same, such events and associated changes in group composition were not recorded. Further, it was not possible to determine gender in this study so that group composition with regards to sex of individuals was not recorded.

This study conducted a fine-scale analysis of behavioral state and fission-fusion dynamics in groups of common dolphins with calves by identifying the factors influencing behavioral state and fission-fusion rate (i.e., group size and spatial cohesion). The total number of calves affected the behavioral state of dolphin groups, giving further insight into the ecology of common dolphins by revealing that not only the presence of calves[15], but also the quantity is an important factor influencing the behavior of common dolphin groups. When considering the varying party composition of common dolphins with calves in other parts of the world[88], the fission-fusion dynamics of *D. delphis* in the South of Portugal may correspond to the most fluid category of Aureli et al.’s (2008) framework. Using UAVs as sampling strategy was effective and gave an advantageous perspective on the animals, while simplifying the behavioral analysis through high-resolution video footage. Future studies with a similar focus should consider this methodology to properly compare results with the present study.

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