Original Investigation

Subadult brown bears (*Ursus arctos*) discriminate between unfamiliar adult male and female anal gland secretion

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ABSTRACT

Olfactory cues have been investigated in social carnivores, many of which use anal/anogenital gland secretion (AGS) for scent marking. However, little is known about how solitary carnivores, such as ursids, use AGS in communication. We hypothesized that subadult (1–3 years) brown bears (*Ursus arctos*) have the ability to discriminate between unfamiliar adult male and female AGS. Confrontations, especially with adult males, carry high risks for dispersing subadults, so they benefit from the ability to assess potential threats based on olfactory cues, including sex, enabling them to avoid risky encounters. We presented AGS from free-ranging adult brown bears (male = 10, female = 10) to subadult brown bears (male = 13, female = 7) in outdoor zoo experiments, and predicted that subadults would avoid male more than female AGS. Neither male nor female AGS were avoided, but subadults quickly habituated to female AGS. However, male AGS was investigated more intensively and the subadults delayed revisiting it. Subadult tended to take longer to complete 6 visits to male than female AGS, which indicated sexual discrimination. We suggest that subadults that store information for the purpose of scent matching in future encounters may reduce their potential costs of conflict based on their prior assessment of the likely outcome of the encounter.

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Introduction

In many mammalian species, olfactory communication, especially scent marks, is the primary form of communication and a key source of information (Wyatt 2003; Müller-Schwarze 2006; Campbell-Palmer and Rosell 2011). Scent marking is a significant form of communication in territorial as well as nonterritorial species (Gorman 1990; Gosling and Roberts 2001; Wyatt 2003), because even solitary species must effectively communicate to maintain their social organization and ensure reproductive success (Bearder 1999). The "sender" of an olfactory cue benefits by advertising its presence to potential competitors and by attracting potential mates. The "receiver" often benefits by scent matching (Gosling 1982; Gosling and McKay 1990). Scent matching allows the receiver to store olfactory information for the purpose of recognizing the sender in the future, which can serve to find a mate or reduce costly encounters, such as escalated physical conflicts (Gosling and McKay 1990; Wyatt 2003). Costs of conflict can be reduced by prior assessment of the likely outcome of an encounter based on the competitive ability of potential opponents (Maynard Smith and Price 1973; Parker 1974; Maynard Smith and Parker 1976).

Olfactory cues have been investigated in several social carnivores (e.g., Asa et al. 1985; Buesching et al. 2002a; Buesching et al. 2002b; Barja et al. 2005; Müller and Manser 2007), and many use anal/anogenital gland secretion (AGS) for scent marking (e.g., Asa et al. 1985; Macdonald 1985; Burgener et al. 2009). Variations in the composition of AGS among conspecifics allow social carnivores to discriminate between males and females (e.g., Jordan et al. 2011), familiar and unfamiliar conspecifics (Drea et al. 2002), and kin and non-kin (Tegt 2004). In contrast, little is known about how solitary carnivores, such as ursids, use AGS in communication, except for the giant panda (*Ailuropoda melanoleuca*). Giant pandas can discriminate AGS from different individuals (Swaisgood et al. 1999), and subadults and adults showed a significant investigative preference for adult over subadult male AGS (White et al. 2003). Brown bears (*Ursus arctos*) possess anal sacs and the secretion of sexually mature adult bears (≥4 years; Zedrosser et al. 2009) may contain a chemical code for sex (Rosell et al. 2011). However, scent marking with AGS by brown bears has not yet been documented.

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Table 1

Subadult (1 and 2 years) captive brown bears in behavioral experiments and that were presented with free-ranging, unfamiliar adult male or adult female anal gland secretion. Experiments were conducted in May–October 2010.

No.	Sex	Age (years)	Location	Date of experiments
1	M	2	Tbilisi Zoo – Tbilisi, Georgia	19–25 May
2	M	2	Tbilisi Zoo – Tbilisi, Georgia	19–25 May
3	M	2	Grönklitt Björnepark – Orsa, Sweden	4–10 June
4	M	2	Grönklitt Björnepark – Orsa, Sweden	4–10 June
5	M	1	Vassfaret Bjørnepark – Flå, Norway	17–23 June
6	M	1	Vassfaret Bjørnepark – Flå, Norway	18–24 June
7	M	1	Copenhagen Zoo – Copenhagen, Denmark	19–25 June
8	M	1	Copenhagen Zoo – Copenhagen, Denmark	20–26 June
9	F	2	Riga Zoo – Riga, Latvia	1–7 July
10	M[a]	2	Riga Zoo – Riga, Latvia	2–8 July
11	M	1	Polar Zoo – Bardu, Norway	4–10 July
12	F	1	Polar Zoo – Bardu, Norway	5–11 July
13	F	1	Ähtäri Zoo – Ähtäri, Finland	6–12 August
14	F	1	Ähtäri Zoo – Ähtäri, Finland	6–12 August
15	M	1	Ähtäri Zoo – Ähtäri, Finland	7–13 August
16	M	1	Borås Zoo – Borås, Sweden	6–12 September
17	M	1	Borås Zoo – Borås, Sweden	7–13 September
18	F	1	Grönklitt Björnepark – Orsa, Sweden	5–11 September
19	F	1	Grönklitt Björnepark – Orsa, Sweden	6–13 September
20	F	1	Karacabey Bear Sanctuary – Karacabey, Turkey	1–7 October

[a] Sterilized.

Brown bears are solitary carnivores with a polygamous mating system (Steyaert et al. 2012) and inter- as well as intrasexual home range overlap (Dahle and Swenson 2003; Støen et al. 2005). Bears are not considered to be territorial, i.e., defending specific areas (Stamps 1994; Schwartz et al. 2003). However, both brown and American black bears (*U. americanus*) may be more territorial than previously thought, because females tolerate more home range overlap with kin than nonkin (Rogers 1987; Støen et al. 2005). Thus, information about kinship and sex may be conveyed in scent marks. Additionally, young male brown bears disperse from their natal areas, probably to avoid mate competition with older bears (Zedrosser et al. 2007), which also suggests sex or age class (subadult vs adult) may be communicated chemically.

Subadult brown bears (1–3 years; after weaning and before becoming sexually mature) disperse during the mating season (May–July). Subadult brown bears have a 15% chance of being killed by conspecifics in Scandinavia (Swenson et al. 2001) and most of these killings occur during the mating/dispersal season. Thus, confrontations with adults have high risks for subadults, because adults could kill them (Mattson et al. 1992; McLellan et al. 1999; Swenson et al. 2001). Moreover, adult males kill subadults more often than do adult females (McLellan 1994). Thus, subadults would benefit from the ability to assess potential threats on the basis of olfactory cues, enabling them to avoid future risky encounters, i.e., by scent matching (Hurst 1990; Hurst 1993; Gosling et al. 1996a; Gosling et al. 1996b).

We hypothesized that subadults could discriminate between unfamiliar adult male and adult female AGS. We predicted that the subadults would avoid male more than female AGS as indicated by the time spent on a preferred side, the frequency of side switches in their enclosures, frequency of visits, duration of visits, time lapses between visits, and the total time of visits to AGS. Additionally, we characterized and compared the investigative, or manipulatory, behavior of subadults toward unfamiliar adult AGS within a familiar setting (their enclosure).

Material and methods

Scent donors

We used AGS from 10 male and 10 female free-ranging adult (≥4 years) brown bears captured in a long-term study by the Scandinavian Brown Bear Research Project (Arnemo et al. 2011). Sex was determined by genital examination. Age of bears that were not captured as yearlings was determined based on cementum annuli in the root of the upper first premolar tooth (Matson et al. 1993). AGS was collected by manually squeezing secretion from the anal sacs (Rosell et al. 2011), during April–May 2008, April 2009, and April 2010, in Dalarna and Gävleborg counties in south-central Sweden (61°N, 14°E). The amount of AGS collected per individual varied from 0.3 to 1 g. AGS was collected in 40 ml glass vials with Teflon-lined caps and stored at −20 °C until taken to zoos.

Zoo experiments

We conducted experiments in 9 European zoos during May–October 2010 (Table 1). Study subjects were male ($n = 13$) and female ($n = 7$) subadult bears (1–3 years; Table 1). Experiments were carried out in a familiar outdoor enclosure and each bear was exposed to 3 experiments at 45 min each: Control 1, Treatment, and Control 2. Treatment was the presentation of either male or female AGS of adult free-ranging brown bears into the enclosure, and Controls 1 (before the treatment) and 2 (after treatment) had no stimulus present. Under normal zoo conditions, bears used in the study were housed with at least 1 bear their age ±1 year. Six bears were also housed with their mothers, 4 of which were also housed with their fathers. We considered the bears housed with their parents to be appropriate for the study, because we investigated responses to unfamiliar AGS. Subadult bears were isolated from penmates during experiments, but whether the penmates remained visible depended upon the facility. We did not habituate bears to isolation prior to data collection. Rather, we held experiments at least 72 h apart to retain the behavior associated with the novelty of isolation. Experiments within subjects were held at the same time of day (±1 h).

Approximately 0.25 g of either male ($n = 10$) or female ($n = 10$) AGS was presented on a rock in the bear's enclosure. Rocks were gathered locally and were recently unearthed to avoid contamination by odors due to exposure. We did not control for rock composition, because geology differed across zoos. We selected rocks with a surface area of approximately 30 cm × 20 cm and deposited AGS in the center. We handled AGS vials with latex gloves and rocks with leather gloves stored in a plastic bag to avoid contamination by human scent. Assignment of male and female AGS

was balanced between sex of the study subjects, and then randomly assigned. Observers did not know which sex of AGS was being delivered. AGS was kept cool or frozen until use.

We video-recorded each experiment (Sony® digital video handycam, model no. DCR-SR35E, Sandefjord, Norway). Experiments were conducted before business hours, except in 2 zoos. In 1 of these zoos, visitors did not approach the bear exhibit during experiments; at the other zoo, bears did not appear to change their behavior when visitors were nearby. Even though visitors had minimal effect on the experiments, we could not control for daily maintenance activities within zoos, such as construction, and human or vehicle traffic near the enclosures.

Side preference and frequency of side switches

After Control 1, the bear's activity was reviewed on video to document its time allotment and to assign a boundary line between a "preferred" and "nonpreferred" side of the enclosure; the "preferred" side being that on which the bear spent the majority of 45 min. Because of the variability in each bear's activity and in zoo enclosures, we could not use a standard time allotment (e.g., "≥30 min") across all bears as the criterion for a preferred side. Each bear's boundary line, as determined in Control 1, remained constant for data collection during Treatment and Control 2. Based on Control 1 observations, the AGS was placed on the preferred side in a location frequented by the bear, in an attempt to shift the bear's preference across the boundary line. We predicted a shift in side preference for bears assigned the male AGS (but not female AGS) during Treatment, and similar time allocation (no shift) during Control 2 relative to Control 1 for male and female AGS.

We also recorded the number of times a bear switched sides during each 45-min experiment. The activity level of a bear may provide insight into its level of anxiety; the more a bear was active, the more anxious it probably was. We predicted more side switches during Treatment by bears assigned to male AGS, and no difference in side switches during Control 2 relative to Control 1 for either male or female AGS.

Frequency of visits, duration of visits, duration of time lapses between visits, and total time of visits

We recorded the frequency of visits to the AGS during Treatment. A "visit" started when a bear's nose came to within 30 cm of the AGS and ended when its forepaws stepped away from the rock. We predicted fewer visits to male AGS.

We also recorded the duration (in seconds (s)) of each visit, as defined above, to AGS. Each visit consisted of at least 1 sniff bout and potentially multiple investigative behaviors (described below). The duration of time that lapsed between visits to AGS, or a "time lapse", was the time (in s) a bear's forepaws stepped away from the rock until its nose again came to within 30 cm of the AGS. Duration of time lapses can be an indication of how long it took bears to process information from the AGS, in addition to how soon more information was sought. "Total time of visits" was the sum of "duration of visits" and "duration of time lapses between visits". We predicted shorter durations of visits, longer time lapses, and shorter duration of total time of visits for male AGS. We only analyzed data for visits during which ≥80% of the study subjects participated.

Frequency of sniff bouts and investigative behaviors

We recorded the frequency of sniff bouts during each visit to AGS. A "sniff bout" was where a bear's nose was within 30 cm of the AGS to when it was 30 cm away from it. Multiple sniff bouts could occur within a visit. Additionally, during each visit we recorded

frequencies of investigative, or manipulatory, behaviors of (a) pawing or stepping on the rock containing AGS, (b) nudging, pushing, or spinning the rock, and (c) rolling the rock; multiple investigative behaviors could occur within a visit. We considered this order of behaviors to be an index of the level of intensity of investigation; sniffing being the least intense, rolling the most intense. Frequencies of investigative behaviors were analyzed for visits where ≥80% of the study subjects participated.

Statistical analysis

We used a Mann–Whitney U-test to examine for significant differences between male and female subjects for each analysis. For only time spent on the preferred side, data were normal and had homogeneity of variance, so we used an ANOVA (e.g., Howell 2007), where Control 1, Treatment, and Control 2 were within-subject factors, and sex of AGS was the between-subject factor. We used a Friedman test to evaluate frequency of side switches across Control 1, Treatment, and Control 2 by male and by female AGS, and a Mann–Whitney U-test to compare frequencies of side switches related to male and female AGS for Control 1, for Treatment, and for Control 2. We used Mann–Whitney U-tests to compare male and female AGS differences in frequency of visits, duration of visits, duration of time that lapsed between visits, and total time to complete visits. We used a linear mixed model (LMM; alpha level was set to 0.05) to examine frequencies of sniff bouts and investigative behaviors. Our model included fixed effects of Treatment, Visit, Behavior, Treatment × Behavior, and Visit × Behavior; study bear ID was fitted as a random effect. Planned pairwise comparisons were made on the estimated marginal means. SPSS software, version 18 (PASW Statistics, IBM, Chicago, IL, USA) was used for all analyses.

Results

There were no significant differences between male and female subjects ($P \geq 0.100$) in side preference, frequency of side switches, frequency and duration of visits, duration of time lapses between visits, and total time of visits. Therefore, we pooled them to examine for significant differences in responses toward male and female AGS.

Side preference and frequency of side switches

Overall, within-subject effects indicated no change in the time spent on the preferred side across the 3 experiments ($F_{(2,36)} = 0.268$, $P = 0.767$). Additionally, there was no change in time spent on the preferred side relative to male or female AGS group assignment (i.e., no interaction effect) ($F_{(2,36)} = 0.066$, $P = 0.936$). Finally, there was no significant difference in between-subject effects (sex of AGS), indicating that the time spent on the preferred side was the same for male and female AGS ($F_{(1,18)} = 0.100$, $P = 0.756$).

There was no significant difference in the number of times bears switched sides during Control 1, Treatment, and Control 2 in the male ($F = 1.590$, $P = 0.491$) or female AGS group ($F = 2.400$, $P = 0.368$), nor significant differences in side switches between male and female AGS during Control 1 (Mann–Whitney $U = 46.000$, $P = 0.782$), Treatment ($U = 49.000$, $P = 0.956$), or Control 2 ($U = 44.000$, $P = 0.668$).

Frequency of visits, duration of visits, duration of time lapses between visits, and total time of visits

All 10 bears made ≥4 visits to male AGS, and 80% made 6 visits. All 10 bears made ≥1 visit to female AGS, 90% made 4 visits, and 80% made 6 visits. A maximum of 12 visits was made to male
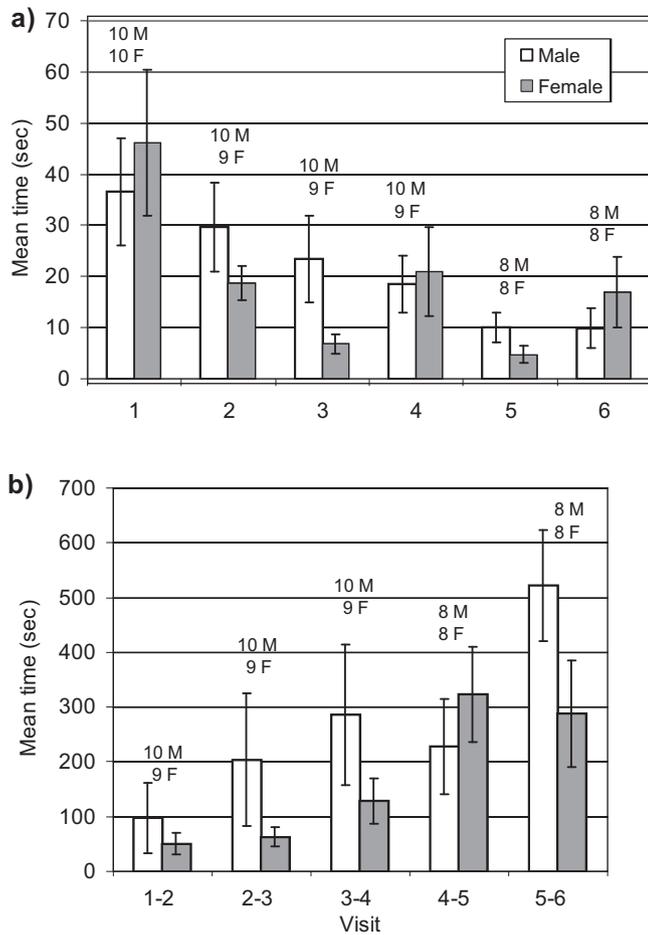
Fig. 1. (a) Mean duration (s) of the 1st 6 visits (±SE) by subadult brown bears (N = 20) (*Ursus arctos*), and (b) mean duration of time (s) that lapsed between the 1st 6 visits (±SE) by subadult brown bears toward male (*n* = 10) and female (*n* = 10) anal gland secretion of free-ranging adult brown bears. Error bars and means are calculated for only the bears participating in visits.

AGS, and a maximum of 20 to female AGS (but a single bear made visits 15–20). There was no significant difference in frequency of total visits between male and female AGS ($U = 39.500$, $P = 0.442$). In general, for both male and female AGS, visit durations gradually decreased in subsequent visits. There was a significant difference between male and female AGS in duration of visit for only visit 3 ($U = 20.500$, $P = 0.026$; Fig. 1a), where visits were longer at male AGS ($X_{male} = 23.400\,s \pm 8.501$ SE, $X_{female} = 6.888\,s \pm 1.882$).

Duration of time lapses increased gradually between subsequent visits for both male and female AGS, but the time that lapsed between each visit 1–6 was not significant between male and female AGS (Fig. 1b). *Post hoc* analysis of female AGS indicated the time that lapsed between visits 4 and 5 was suggestively and almost significantly longer than that for visits 3–4 (Wilcoxon signed-ranks test; $Z = -1.820$, $P = 0.056$). For male AGS, the difference in time that lapsed between visits 4 and 5 and 5–6 was not significant; there were no significant differences in time lapses between any of the immediately prior time lapses for male AGS.

The total time to complete 6 visits (visit durations + time lapses) was again suggestively, close to significantly, different between male and female AGS ($U = 26.000$, $P = 0.074$). Bears took on average 8 min longer to complete 6 visits to male AGS in comparison to female AGS ($X_{male} = 1311.200\,s \pm 182.892$, $X_{female} = 811.900\,s \pm 189.841$).

Frequencies of sniff bouts and investigative behaviors

Investigative behavior almost always occurred in the same order: directly sniffing the AGS and sniffing upwardly in the air, followed by pawing or stepping on the rock containing AGS, then nudging or pushing the rock, and in some cases eventually flipping or rolling the rock. There were significant differences in frequency of sniff bouts between male and female subjects during only the 1st of 6 visits ($U = 17.500$, $P = 0.021$), where female subjects made more sniff bouts than male subjects ($X_{males} = 2.308 \pm 0.511$, $X_{females} = 3.857 \pm 0.404$); and in frequency of rock rolls for only the 4th of 6 visits ($U = 21.000$, $P = 0.044$), where male subjects rolled rocks more than female subjects ($X_{males} = 0.833 \pm 0.297$, $X_{females} = 0$). There were no significant differences ($P > 0.100$) between male and female subjects in frequency of paw/step or nudge/push.

Pairwise comparisons of Treatment × Behavior for male AGS indicated that only rolls occurred significantly less frequently than other behaviors (sniff bout vs. roll: Mean Difference (MD) = 1.220 ± 0.360 SE, df = 389.550, $P < 0.001$; nudge/push vs. roll: MD = 0.779 ± 0.360, df = 389.550, $P = 0.031$; paw/step vs roll: MD = 0.915 ± 0.360, df = 389.550, $P = 0.012$). All other pairwise comparisons (sniff bout vs. paw/step, sniff bout vs. nudge/push, paw/step vs. nudge/push) were nonsignificant (all $P > 0.100$), hence these behaviors occurred in similar frequencies. Pairwise comparisons of Treatment × Behavior for female AGS indicated that rolls occurred significantly less frequently than sniff bouts and paw/step (sniff bout vs. roll: MD = 1.360 ± 0.370, df = 389.550, $P < 0.001$; paw/step vs roll: MD = 1.586 ± 0.370, df = 389.550, $P < 0.001$). Likewise, nudge/push occurred less frequently than sniff bout (nudge/push vs. sniff bout: MD = 0.891 ± 0.370, df = 389.550, $P = 0.017$) and paw/step nudge/push vs. paw/step (MD = 1.118 ± 0.370, df = 389.550, $P = 0.003$). All other pairwise comparisons (sniff bout vs. paw/step, sniff bout vs. roll) were nonsignificant (all $P > 0.100$), hence these behaviors occurred in similar frequencies. Thus, the male AGS elicited a higher intensity level of physical contact (up to nudge/push) than female AGS (up to paw/step).

Discussion

The data supported the hypothesis that bears differentiate between male and female AGS. We initially predicted that duration of visits would be shorter for male than female AGS; however, there were no significant differences for any visit, except visit 3, and the opposite outcome occurred: visit duration was longer for male AGS. We also predicted that the duration of time lapses would be longer for male AGS than female AGS, which was not supported. *Post hoc* considerations of visit durations to female AGS strongly suggested a decreased interest by the 3rd visit, and that subadults lost interest after visit 4. For male AGS, the absence of significant differences for duration of visits or duration of time lapses suggested male AGS remained interesting through 6 visits. However, it is unknown if subadults acquire new information at each visit or simply re-enforce the information gathered previously. In contrast, subadult bears seemed to collect most of the important information from female AGS on the 1st visit and were habituated to it by visit 4.

We also predicted that the total time to complete visits would be shorter for male AGS, however, subadults tended to take longer to complete 6 visits to male AGS. This suggests that subadults took more time to collect information from male AGS and did not return quickly, a likely demonstration of cautious behavior. Several studies have demonstrated chemical differences in scent between male and female giant pandas (Hagey and MacDonald 2003; Yuan et al. 2004;

Liu et al. 2006; Zhang et al. 2008). Rosell et al. (2011) documented a significant difference in the abundance of certain chemical compounds in the AGS of male and female brown bears, which may have been what the subadult bears in our study responded to. In turn, this suggests that male AGS may communicate different messages than female AGS.

Based on the difference in time spent collecting and processing information (i.e., cumulative time to complete 6 visits), we suggest that subadults were able to discriminate male from female AGS. Also giant pandas discriminated the sex of a signaler (Swaisgood et al. 2000). Our results suggest that discrimination of adult male and female AGS is a temporal process for subadults, where duration of visits *in addition to* the time between visits influences behavior. This makes sense for subadults, because the more information collected (duration of visits), the better equipped the subadult will be in future encounters; and the more cautious the subadult is while collecting information (duration of time lapses between visits), the better the chance to detect immediate potential risks in the vicinity.

Our prediction that male AGS would be avoided (i.e., fewer and less intensive investigative behaviors) was not supported. For female AGS, frequencies of sniff bouts and paw/steps were similar, whereas for male AGS, frequencies were similar for sniff bouts, paw/step, and nudge/push. This meant male AGS elicited a higher-intensity level of investigation. Higher-intensity investigation of AGS would presumably arm subadults with more information for use in scent matching.

In our study, male AGS was not avoided. In a solitary social system, avoidance could be equivalent to "ignorance," or lack of information, which could be detrimental. Thus, contrary to our predictions, avoidance of adult male AGS may not benefit subadults, rather, subadults may benefit by arming themselves with as much information as possible about other individuals, particularly those of high risk, i.e., adult males. Subadults that store information for the purpose of scent matching in future encounters may reduce their potential costs of conflict based on their prior assessment of the likely outcome of the encounter (Maynard Smith and Parker 1976; Gosling and McKay 1990).

Acknowledgements

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